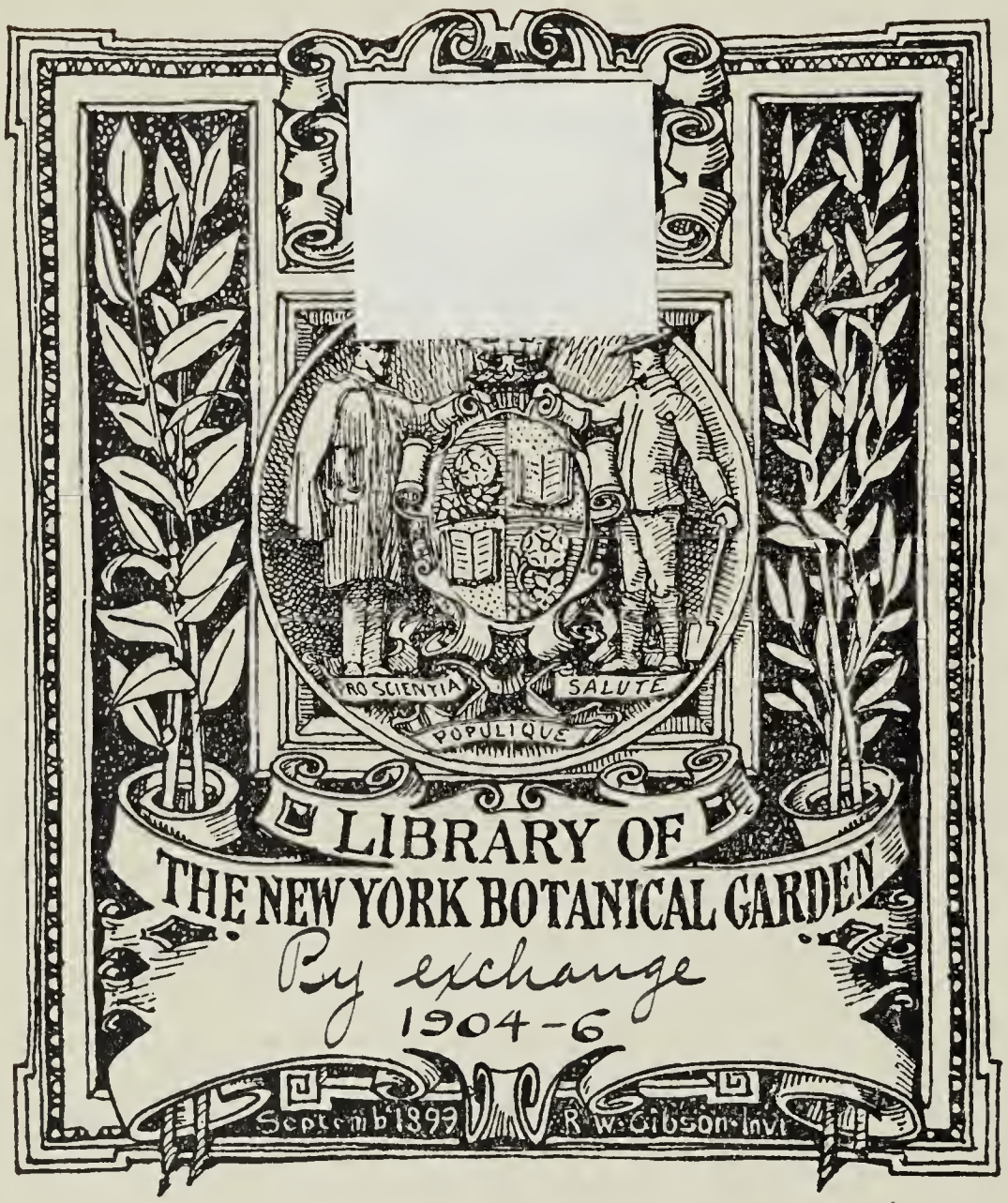
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PROCEEDINGS

OF THE

Boston Society of Natural History.

VOL. XXXII.

WITH FORTY-EIGHT PLATES.

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PROCEEDINGS OF THE ANNUAL MEETING, MAY 4, 1904.

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October, 1904.

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No. 1. — PROCEEDINGS OF THE ANNUAL MEETING, MAY 4, 1904.

REPORT OF THE CURATOR, CHARLES W. JOHNSON.

During the past year while working on the various collections in the Museum, one thought has been uppermost, and that is, how to display the New England fauna to the best advantage. This question was not fully solved until the four large cases of mammals which obstructed the main floor, were removed. These cases were like heavy clouds obscuring everything else, and when they were taken away light spread over the whole situation.

A special collection to be useful or effective should be arranged with some continuity. To accomplish this, two things must be considered: first, the amount of space required, and second, the general plan of the Museum. We find that the rooms situated in four angles of the building are too small, poorly lighted, and with no available space for horizontal cases unless the collection should be greatly scattered. We also find that to obtain the requisite space in these rooms would require an enormous amount of rearrangement and unnecessarily alter the present arrangement of the Museum.

A plan was submitted to and approved by the Museum committee whereby the New England collection will occupy all of the wall cases of the main floor and the entire main gallery. New England paleontology will be placed in the extreme eastern end between the two rooms devoted to American and foreign paleontology, while the remaining space will be given to the birds and mammals. On the gallery will be arranged the reptiles, batrachians, fishes, and all of the invertebrates. Thus that which is to be the leading feature of the Museum will also be the most prominent and occupy a central position from which all portions of the general collection will diverge.

Mammals and Birds.

To make room for the mammals in the cases above referred to, it was necessary to reduce the number of birds on exhibition. The

services of Mr. C. E. Brown were secured and over 2500 duplicates or undesirable specimens were unmounted and packed away as skins in storage cases. This enabled us to place all of the general collection of birds on the upper floor; then by removing the New England Mollusca, etc., to the main gallery all of the mammals were brought together in room M.

During the year Mr. Brown has been occupied in securing desiderata and in making some preliminary groups of the more common birds. Small groups have been prepared showing the male and female, with nest and eggs, of the cedar bird, red-eyed vireo, Baltimore oriole, kingbird, catbird, red-winged blackbird, and black-billed cuckoo. Six additional birds were secured for the New England collection, including two evening grosbeaks, the first obtained in this section since 1890; nests and eggs of the red-breasted merganser and herring gull from Ship Island, Moosehead Lake, were also added. A handsome specimen of the Carolina dove, from Barnstable, was presented by Miss A. T. Handy, and a female ring-necked duck, from Eastham, was donated by Mr. Dwight Blaney. Nests and eggs of the summer yellowbird, American goldfinch, song sparrow, and olive-backed thrush were presented by the Nuttall club. Two black swans were presented by Mr. Arthur A. Brigham.

Among the mammals added to the collection is a fine example of the Virginia deer, shot by Mr. Brown at Moosehead Lake; also a mink, muskrat, red bat, and a group of chipmunks. A specimen of *Lynx ruffus*, shot near Southampton, Mass., was presented by Miss Eleanor P. Rathbun, and a large brown bat by Mr. Lawrence Brooks. All the bats have been mounted on plate glass. Mr. Allen has done considerable work on the skeleton of *Mesoplodon bidens* preparatory to mounting.

Fishes, Reptiles, etc.

This collection has been increased by 20 fishes and 15 reptiles and batrachians, including a Blanding's tortoise from Tyngsborough, Mass., presented by Mr. Frederick Blanchard, and a box tortoise from the same locality, presented by Mr. M. L. Knight. A large spotted salamander (*Amblystoma punctatum*) was presented by Mrs. Augustus Hemenway, and several snakes from Lake Cham-

plain by Mr. Roland Hayward. Among the fishes may be mentioned the togue or great lake trout from Moosehead Lake and two *Macrura bairdii*, a deep sea species, obtained in exchange from the Museum of comparative zoology.

Insects.

Through the generous cooperation of the members of the Cambridge entomological club and others, I am able to report very favorably on this department. Mr. Roland Hayward has donated a handsome cabinet of forty-five drawers with about 450 species of Coleoptera. The cabinet is well adapted for the study collection of New England Lepidoptera and will be used for that purpose. Mr. A. P. Morse presented upwards of 225 species of Diptera and 135 species of Hemiptera-Heteroptera. This valuable collection, together with about 50 species of Diptera received through Mr. Henshaw, 60 species presented by Mr. C. A. Frost, and 280 presented by the Curator, combined with the material collected during the past season, has made a very creditable showing in the study collections of Diptera and Hemiptera. The former is arranged in 45 Schmitt boxes, containing at present 686 species. The latter in 10 boxes, contains 172 species.

Mr. L. W. Swett has donated his entire collection of New England butterflies, consisting of 57 species and 121 specimens, most of which have been placed in the study collection. The exhibition series has been rearranged in 7 glass covered boxes. Mrs. Annie T. Slosson has kindly donated about 90 species of White Mountain insects. Through Mr. Jacob Doll, of the Brooklyn museum, 96 species of inflated Lepidopterous larvae and pupae were obtained in exchange for a collection of 370 species of Diptera given by the Curator. From Mr. H. M. Parshley were received in exchange 125 species of local Coleoptera and Hemiptera, and from the Connecticut agricultural experiment station a number of Diptera.

Specimens have also been received from Messrs. G. M. Allen, P. G. Bolster, Owen Bryant, J. A. Cushman, W. D. Denton, J. H. Emerton, Abner Hatfield, H. H. Newcomb, S. A. Shaw, F. Sherriff, and Wm. L. Underwood. The Curator's summer field work was confined principally to the Diptera, Hemiptera, and Hymenoptera.

Over 6,000 specimens were collected, of which the Hemiptera-Homoptera and the Hymenoptera have not yet been studied.

Molluscs.

Work on the general collection has continued, and most of the Prosobranchs have been gone over, including those in the Mayo collection which are being studied conjointly with those on exhibition. Species desirable for the exhibition collection are selected, and the remainder incorporated into the study series. In this work I have had valuable assistance from Miss Martin, who is cataloging the Mayo collection as soon as it is classified and arranging and fastening all shells and labels on the tablets. At other times Miss Martin has been at work on the study collection of Gastropods, placing them in new trays, the smaller species in glass tubes, bringing together the scattered species and rearranging the entire series to conform with those on exhibition. The glass models of the Nudibranchs have been carefully unmounted and prepared for rearrangement. Miss Martin has also been over the alcoholic material replenishing where necessary.

The New England Mollusca have been rearranged by Mr. Cushman in the railing case of the main gallery. This collection has been greatly augmented by large suites from the Roper collection. The distribution of many of the species has been studied and shown on small maps placed in the case. Mr. Cushman has also carried out this feature in rearranging the echinoderms. Mr. Owen Bryant has presented over 50 species of shells from New England and the Bermudas. Specimens have also been received from Messrs. J. A. Allen, F. N. Balch, Dwight Blaney, J. A. Cushman, C. A. Davis, Miss M. K. Bachelder, and the Curator.

Paleontology, etc.

In this department great credit is due to Mr. J. A. Cushman for his efficient and valuable work. Mr. Cushman has been over the entire collection of American fossils, relabeling, rearranging, and bringing all of the New England material together. He has also worked over the study series and arranged it in geological sequence.

In going over the collections, special attention was given to locating and designating types, figured or mentioned specimens, the number of lots referable to this class being 163. A card catalogue of these has been made, and a catalogue of the types, etc., will be published as soon as the foreign collection has been studied.

In company with Dr. R. T. Jackson, Mr. Cushman visited the fossiliferous deposits of Gay Head, Martha's Vineyard. He discovered the layer containing the fossil crabs and obtained what is perhaps the best series extant, and also obtained a number of fossil plants, shark teeth, etc. Mr. Cushman has also labeled and placed on exhibition a representative series of the Eocene fossils donated by Rev. L. T. Chamberlain and referred to in my last report. The collection contains about 550 trays. A series of specimens etched out by acid, from the white limestone of Nahant, was presented by Mr. John M. Sears. The Curator has donated a number of Pliocene fossils from Florida, and a fish from the Trias at Boonton, N. J. Twenty-six specimens of New England minerals were received from Mr. J. C. Rand, and a fine example of garnetiferous gneissic rock from Naples, Me., was presented by Mr. Eli S. Weeman.

Botany.

During the year Miss Carter has continued her work of revising the entire herbarium. Some 18 orders have been gone over including from the Leguminosae to the Ficoideae and a portion of the Umbelliferae. The exhibition series has also been revised and dusted. Fifteen persons have consulted the herbarium. Specimens have been received from Messrs. J. A. Cushman, J. A. Wheeler, F. E. Allen, and Miss Cora H. Clarke. Forty North American lichens were obtained by purchase.

Mrs. J. M. Arms Sheldon has added a number of species to the Synoptic collection, and has placed numbers on all of the specimens which correspond with those given in the guide to the invertebrates, the manuscript of which is ready for publication.

The Museum has been well patronized on public days, while on other days it has been visited by 451 pupils representing 16 schools. Material for study has been loaned to twelve persons.

REPORT OF THE CURATOR OF THE TEACHERS' SCHOOL OF SCIENCE, PROF. GEORGE H. BARTON.

Lowell Free Courses.

Field Courses.

These consisted, as during the past three years, of three definite courses of instruction, botany, zoology, and geology. The object of each course is to train the members of the class in making observations and investigations in the field. Although there is no direct connection between the field and the laboratory courses, the former distinctly supplement the latter and those who take both derive a much greater benefit from the work. There are so many, however, who cannot take both, that it is considered advisable to keep them as separate courses.

Field work, especially where a large percentage of the class consists of women, is affected strongly by the weather. During the past year there were many stormy or partially stormy Saturdays, which produced a very fluctuating attendance. Each course consists of ten lessons in the spring and a like number in the autumn.

Botany.— This course, in charge of Mr. Hollis Webster, during the spring had an average attendance of 26.2; the largest number present at one time being 44, the smallest 7. The average attendance during the autumn was 21.8; the largest at one time being 29, the smallest 13.

Special attention was given to the Thallophytes, especially the fungi, as this group had been studied in the classroom during the winter. At the same time trees and shrubs, as well as other plants, were always under observation.

The brief key to orders and genera of the fungi by Prof. E. H. Burt was used by the class. It was constantly an aim to demonstrate the availability of such plants as came under observation for purposes of class instruction.

The following places were visited: Hammond's woods at Chestnut Hill (three times), Norumbega Park, Blue Hill Reservation, Salem pastures, Lowell Junction, Arnold Arboretum (twice), Cohasset, sandplains and dunes at Ipswich (twice), Purgatory swamp, Cunningham woods at East Milton, Lynn woods, Muddy

Pond Reservation at Hazlewood, Middlesex Fells, Arlington, and Stony Brook.

The lessons for the present spring began on April 23d with an attendance of 51. About 70 have enrolled as members of the class. These lessons will deal particularly with the mosses, ferns, and related plants. Other topics will be treated as occasion offers.

Zoology.—This course in charge of Mr. Albert P. Morse, Curator of the zoological museum, Wellesley college, had during the spring an average attendance of 26. The largest number attending at one time was 43, the smallest 7. During the autumn the average attendance was 17.2, the largest number being 23, the smallest 14.

The spring lessons included outdoor observation of the animals studied during the winter, insects, bird-life including changes of plumage (76 species being observed), tracks of animals, and a special lesson on spiders which was kindly contributed by Mr. J. H. Emerton.

The localities visited were chiefly in the city parks and the Metropolitan Reservations near at hand, but two for special purposes were at a greater distance, Cohasset and Ipswich.

In the autumn lessons the topic of protection, including special protective devices and coloration in relation to backgrounds, direction of light, enemies, and friends, was studied in the field and museum with the aid of demonstrations. This subject proved of great interest to the class. The localities visited were included mostly in the parks and reservations; two lessons, owing to the highly inclement weather, were given in the Museum of comparative zoology at Cambridge.

The lessons for the present course began on April 23d with an attendance of 47.

Geology.[1]— This course is in charge of the Curator of the School. During the spring there was an average attendance of 52.1. The largest number present at one time was 83, the smallest 17. For the autumn the attendance varied from 36 to 116, with an average of 59.1.

During the spring a portion of the lessons was devoted to a study of minerals in direct continuation of the winter's work in the classroom. Fitchburg, Newburyport, and Bolton were especially visited

[1] This is not a Lowell Course, but is supported by a friend of the Society.

for this purpose. The remainder of the lessons was devoted to a study of the structural features of constructional types of topography, as eskers, terraces, lake beds, and drumlins. The localities visited for this purpose were in the immediate neighborhood of Boston. One extended trip was made to Mount Holyoke and Mt. Tom in the Connecticut valley, taking nearly three days for the complete lesson.

The lessons during the autumn included five upon constructional topographical features, drumlins, terminal moraines, kettle holes, and lake beds. The remaining five were devoted to structural features of the solid crust, stratification, dikes, and intrusive beds.

These lessons were all consecutive parts of a regular four years' course. The places visited were Orient Heights, Arlington, Rockport, Clinton, Cambridge, Somerville, Roxbury, Winter Hill, Newton Center, and in an extended trip of two days, the Hoosac and Greylock mountains. The spring course for the present year has opened with an attendance of 108.

Laboratory Courses.

Each of the laboratory courses, botany, zoology, and geology, consists of a series of fifteen lessons of two hours each during each year for four years, a total of sixty hours for each course. Very commonly, as is the case this year, sixteen lessons are given exclusive of the final examination. Short examinations are given at each exercise and at the end of each year a final examination of three hours is given. Those members who have passed satisfactory examinations during the four years receive a diploma stating the kind and amount of work accomplished.

The small size of the laboratory, only 50 seats, in which the botany and zoology lessons are given, necessarily limits the number receiving tickets to these courses. Unfortunately some of those receiving tickets find the work too difficult for their previous training, and consequently drop out after the first few weeks; others are kept out by sickness, so that by the end of the term not even the small number of seats is filled even though many applicants were denied tickets at the beginning of the course.

Botany. — This course in charge of Mr. Webster, assisted by Miss Jennie F. Conant, began its third year on November 21st,

and ended on March 26th. Of about 70 applicants, 50 received "A" tickets, which entitle the holder to a seat, and 6 received "B" tickets, which entitle the holder to a seat if one is vacant a short time after the beginning of the lesson. The average attendance was 37.4. The low average is due to several very stormy Saturdays on some of which it was almost impossible for those living out of town to get in to the lesson. The lowest attendance was 19, on January 9th, when a severe snow storm nearly prevented traveling. The final examination was taken by 27.

The subjects taken up during the winter were the Bryophytes and the Pteridophytes. Common and easily obtained representatives of the mosses, ferns, and related plants, such as teachers are likely to meet and should know, were studied. The plants were studied, first, as to structures and life history; second, as to relationship; and third, as to generic and specific characteristics. The material was supplemented by numerous prepared slides. All members of the class were provided with a general textbook, and Grout's "Mosses with a Hand Lens" was required.

The work of next year will be on Gymnosperms and Angiosperms. Volunteers from the class, under direction of the instructor, are to collect flowering plants for use next winter.

As the work is largely with the microscope much individual help and instruction is needed which could not be given without the presence of a trained assistant. Much credit is due Miss Conant without whose intimate acquaintance with the subject and with the methods of teaching it much of the value of the lessons would have been lost.

Zoology.— This course under Mr. Morse, assisted by Miss M. E. Cherrington, began on November 21st, and ended on March 26th.

The average attendance for the term was 38.5, a slight increase over that of last year in spite of the exceptionally severe storms of this season. The weekly tests were taken by 25 and the final examination by 19, the average rank obtained being about 79 per-cent.

The lessons were devoted to the Arthropoda, chiefly Crustacea and Insecta. Much interest was aroused in the study of insects and as this subject is especially valuable to teachers, a special request was made to take up a further study of this subject next winter. As about four fifths of the class prefer this arrangement it will probably be made.

In addition to the regular work on Saturdays, ten or twelve members of the class have expressed a wish for supplementary work to be done either on evenings or at other suitable times.

As an addition to the outfit of this department several models of insect mouth-parts have been presented by Mr. J. H. Emerton to whom much credit is due for this gift and for his general interest in this branch of the work.

Geology. — This course, given by the Curator of the School, took up the subject of lithology, the second in the four years' course. The first two lessons comprised a general review of the rock forming minerals. The remaining fourteen lessons were devoted to lithology proper in which all the common species of rocks, 42 in all, were studied. The method of instruction was partly by lecture and partly by individual work with specimens. A sufficient number of specimens was provided to enable each two persons to have a complete set of the species and varieties studied at each lesson. By this method each person was able to study about 180 specimens during the term. Beside the specimens used in the class work many large ones were used on the lecturer's table, and the collections of the Society were much visited by members of the class.

The lecture hall, which is used for this course, has a seating capacity for class work of 100. By making two divisions, a forenoon and an afternoon, as has been done for the last two years, there is a possibility of accommodating 200. All applicants, numbering 182, were given tickets. The average attendance for the term was 123.8. Of these 55 were not absent a single lesson, and 15 were absent but once. The weekly tests were taken by 101, and the final examination was taken by 80. The same facilities for extra work have been offered this year as last year. Sets of rock specimens have been provided for study in the basement laboratory and members of the class have been allowed to study there during the week. Especially on days when the schools had but one session the room was freely used. The same room has also been kept open one night a week under the direct charge of the Curator of the School, making 21 nights in all.

The average attendance from December 7 to April 30 was 27.8 per week, including all extra day work and that of one evening. This shows the definite call for this kind of work. It is hoped to extend it also to the classes in botany and zoology.

Summer School.

Owing to the inability of the Curator to give his time, there was no regular summer work. Hereafter it is intended to make the summer school a definite feature. This coming summer an extended trip is arranged to include work in the Yellowstone Park, among the active and extinct volcanoes of Hawaii, and the glaciers of the Selkirk mountains.

Special Work.

The Curator of the School has spoken before teachers' organizations and before the teachers and pupils of various schools on both geological and geographical subjects usually fully illustrating the lectures with the lantern. The principals of the public schools consider this as a valuable addition to the work of the School.

Two members of the class in Geology have begun original investigations in the field under the direction of the Curator. It is expected that others will also take up original work during the coming year.

Improvements.

A large number of specimens, trays, and other materials have been added to the teaching collections.

Many firms publishing textbooks of science have very generously furnished copies of the latest works in botany, zoology, geology, and chemistry. By this means the School now has a small library in which the teachers can find and inspect the latest textbooks in natural science.

In conclusion the Curator of the School would like to express his high appreciation of the ability and success with which the instructors in botany and zoology have conducted their classes, as testified by very many of the members of each class. A constant offer on the part of members of the classes to contribute toward the expenses shows their appreciation of the value of the work.

To Prof. A. Lawrence Lowell, to the friend of the Society, and to the officials of the Society the School owes a deep debt of gratitude for their cordial cooperation in the conduct and improvement of the School.

REPORT OF THE SECRETARY AND LIBRARIAN, GLOVER M. ALLEN.

Membership.

During the year 1903–1904, the Society has lost by death five Corresponding Members — Charles E. Beecher, Hermann Behr, Augustus R. Grote, J. Peter Lesley, and Karl A. Zittel. Seven Corporate Members have also died during the year — Charles W. Galloupe, Francis C. Gray, Nathan B. Prescott, Gen. Alfred P. Rockwell, Charles J. Sprague, Andrew G. Weeks, Samuel Wells. Charles W. Galloupe and Charles J. Sprague were also Patrons. Nine Corporate Members have resigned.

Twenty-seven new Corporate Members have been elected during the year, so that the total gain in membership for the year is but 6. The names of these new members and the dates of their election are as follows: —

Michael J. Ahern, March 11, 1904.
Arthur C. Bradley, March 11, 1904.
Walter R. Brinckerhoff, M.D., December 16, 1903.
C. Emerson Brown, March 11, 1904.
Edward S. Bryant, November 13, 1903.
Owen Bryant, November 13, 1903.
John T. Coolidge, 3d, March 11, 1904.
Philip T. Coolidge, December 16, 1903.
George V. N. Dearborn, M.D., April 22, 1904.
Frank S. Elliott, November 13, 1903.
Richard S. Eustis, March 11, 1904.
Miss Margaret C. Ferguson, April 22, 1904.
George A. Fisher, March 11, 1904.
Elisha Flagg, M.D., March 11, 1904.
Edward C. Jeffrey, April 22, 1904.
Douglas W. Johnson, December 16, 1903.
Clarence C. Little, March 18, 1904.
Harvey M. Mansfield, April 22, 1904.
Nathaniel C. Nash, Jr., April 22, 1904.
Charles S. Rackemann, March 11, 1904.
Alfred Rehder, April 22, 1904.

Philip L. Saltonstall, March 11, 1904.
Hervey W. Shimer, December 16, 1903.
Ewing Taylor, M.D., December 16, 1903.
Goodwin Warner, March 18, 1904.
Miss Alice W. Wilcox, November 13, 1903.
Leonard W. Williams, November 13, 1903.

The revised list of members, May 1, 1904, consists of 8 Honorary, 118 Corresponding, and 465 Corporate Members; a total membership of 591. There are 14 Patrons.

Meetings.

Fourteen regular meetings of the Society have been held during the year. The number of persons present at any one meeting has varied from 21 to 149, the average attendance being 55, as against 50 for last year.

The total attendance for the year is 770. Fifteen formal communications have been made during the year by as many persons, of whom three had not previously spoken before the Society. Eleven papers have been presented by title.

The meetings, attendance, and communications have been as follows: —

May 6, 1903. Annual meeting. Forty persons present.
Reports of the Curator, Curator of the Teachers' school of science, Secretary, Librarian, Treasurer, Trustees.
Mr. James H. Emerton. Animal tracks in the sand.
Dr. M. T. Thompson. The metamorphoses of the hermit crab. (By title.)

May 20, 1903. General meeting. Twenty-four persons present.
Prof. Edward S. Morse. Some Florida land snails.
Prof. John S. Kingsley. A New England sea anemone.
Mr. John P. Munson. The development of the ovum in the turtle. (By title.)

November 4, 1903. General meeting. One hundred and ten persons present.
Prof. William M. Davis. Notes on a journey in Turkestan.
Mr. R. G. Leavitt. Trichomes of the root in vascular Cryptogams and Angiosperms. (By title.)

Dr. Richard S. Lull. Fossil footprints of the Jura-Trias of North America. (By title.)

Miss Ethel M. Mc Clenahan. The development of the rostrum in Rhynchophorous Coleoptera. (By title.)

November 18, 1903. General meeting. Sixty-four persons present.

Prof. W. O. Crosby. Geological observations in Alaska.

December 2, 1903. General meeting. Forty-nine persons present.

Prof. George Wharton James. The Hopis and their snake dance.

December 16, 1903. General meeting. One hundred and forty-nine persons present.

Mr. William Lyman Underwood. Biography of a black bear and some experiences with a bay lynx.

January 6, 1904. General meeting. Thirty-one persons present.

Mr. Reginald Heber Howe, Jr. Birds of the central and eastern coast regions of Florida.

Dr. B. L. Robinson. Contributions from the Gray herbarium of Harvard university. New series.—No. 27. (By title.)

January 20, 1904. General meeting. Fifty-nine persons present.

Prof. George H. Barton. The summer school of the Teachers' school of science in Nova Scotia.

February 3, 1904. General meeting. Fifty-four persons present.

Miss Margaret C. Ferguson, Ph. D. The development of the gametophytes, fertilization, and related phenomena in Pinus.

Mr. Leon J. Cole. Report on Pycnogonida collected at Bermuda in the summer of 1903. (By title.)

Mr. Harold Bowditch. A list of Bermudan birds seen between July 6th and August 22d, 1903. (By title.)

Prof. W. R. Coe. The structure and development of the terrestrial Nemertean (*Geonemertes agricola*) of Bermuda. (By title.)

February 17, 1904. General meeting. Twenty-one persons present.

Prof. J. B. Woodworth. Some vertebrate footprints from the carbonic system in Massachusetts.

Dr. G. P. Clinton. North American Ustilagineae. (By title.)

March 2, 1904. General meeting. Forty-six persons present.

Prof. A. Lawrence Rotch. Physical and physiological observations on Mt. Blanc.

March 16, 1904. General meeting. Thirty-six persons present.

Prof. Edward L. Mark. The Bermuda biological station for research. Summer of 1903.

April 6, 1904. General meeting. Forty-six persons present.

Dr. Hans Gadow, F. R. S. The physiological and physical aspect of animal coloration.

April 20, 1904. General meeting. Forty-one persons present.

Prof. William H. Niles. How the Asiatic situation is affected by geographic conditions.

Mr. Dwight Blaney. A list of the shell-bearing Mollusca of Frenchman's Bay, Maine. (By title.)

Publications.

During the year the following publications have been issued: —

The comparative anatomy and phylogeny of the Coniferales. Part 1.—The genus Sequoia. By Edward C. Jeffrey. Memoirs, vol. 5, no. 10, 19 pages, 4 plates.

Fossil footprints of the Jura-Trias of North America. By Richard Swann Lull. Memoirs, vol. 5, no. 11, 97 pages, 1 plate, 34 text figures.

Proceedings of the annual meeting, May 6, 1903. Proceedings, vol. 31, no. 2, 38 pages.

Systematic results of the study of North American land mammals during the years 1901 and 1902. By Gerrit S. Miller, Jr., and James A. G. Rehn. Proceedings, vol. 31, no. 3, 85 pages.

The metamorphoses of the hermit crab. By Millett T. Thompson. Proceedings, vol. 31, no. 4, 53 pages, 7 plates.

Observations on the cytology of *Araiospora pulchra* Thaxter. By Cyrus Ambrose King. Proceedings, vol. 31, no. 5, 35 pages, 5 plates.

Contributions from the Gray herbarium of Harvard university. New series.—No. 27. By B. L. Robinson. Proceedings, vol. 31, no. 6, 25 pages.

Trichomes of the root in vascular Cryptogams and Angiosperms. By Robert Greenleaf Leavitt. Proceedings, vol. 31, no. 6, 41 pages, 4 plates.

A price list of the publications for sale by the Society has also been prepared and printed.

Under the editorship of Mr. Samuel Henshaw, there have also been published the first two parts of volume 7 of the Occasional Papers. It is proposed to devote this volume to a series of lists of the animals of New England, and the first two parts containing the Reptilia, 13 pages, and the Batrachia, 10 pages, have been prepared by Mr. Henshaw.

Library.

The additions to the library during the year have been as follows: —

	8vo.	4to.	Folio.	Maps.	Total.
Volumes	1660	353	32		2045
Parts of volumes	3928	845	22		4795
Pamphlets	6715	639	36		7389
Maps				200	200
Total	12,303	1837	90	200	14,429

The S. H. Scudder library, included in the above, contains:—

	8vo.	4to.	Folio.	Maps.	Total.
Volumes	1127	232	25		1384
Parts of volumes	350	154	19		523
Pamphlets	5936	605	19		6560
Maps				148	148
Total	7413	991	63	148	8615

The Society has also received from Mr. Scudder 886 duplicates (mostly pamphlets) which were kept to replace former copies. There were also 278 works by himself, about half of which are new to our shelves. A special book plate has been made for the books of the Scudder library.

A little more than one fourth of all the books and pamphlets received from Mr. Scudder are upon the shelves ready for use. The rest have been compared with the catalogue and entered in the accession catalogue. The great task of cataloguing this library has been performed with care and thoroughness by the assistant librarian, Miss Harriet Biddle.

The Society has also received from Miss M. E. Blatchford an oil portrait of Mr. Scudder, which has been hung in the library with those of other former presidents of the Society. Miss Blatchford has also presented many of the original drawings for Scudder's Butterflies of New England.

From the bequest of Mr. R. C. Waterston we received 70 volumes in addition to those received several years ago.

From the Cambridge entomological club we have received: —

	8vo.	4to.
Volumes	21	
Parts of volumes	1295	201
Pamphlets	263	
Total	1579	201

The parts of volumes include 88 volumes completed. Among these may be mentioned complete sets of the Illustrierte wochenschrift für entomologie, Illustrierte zeitschrift für entomologie, and Allgemeine zeitschrift für entomologie; and the Entomologist's record and journal of variation (except one or two numbers); also The Naturalist (London) from 1884 to date; and 17 volumes of The Entomologist, of London.

The increase of the library has made necessary the installation of a new bookcase in the basement room, in order to allow for the spreading out of the journals in the front library.

Three new exchanges have been added during the year: Biologisches anstalt auf Helgoland, Kiel; Biological society of Washington; Journal of geography. Two others are pending, and one has ceased. The exchanges now number 454.

During the year, 839 volumes and 2322 pamphlets have been bound; of these, the pamphlets and 131 volumes are a part of the S. H. Scudder library.

Eight hundred and fifty-nine books have been borrowed by 107 persons; 421 books have been borrowed for use in the building. The library has been consulted about 265 times.

The library contains, May 1, 1904, 30,497 volumes, 1606 current or otherwise incomplete volumes, and 23,234 pamphlets.

Walker Prizes.

The subjects selected by the Walker Prize committee for the annual award were: —

1. The reactions of organisms to solutions, considered from the standpoint of the chemical theory of dissociation.
2. Relations of plants to electricity.
3. A statistical study of the relative cross-fertility between the varieties of a species.
4. The chemical and physical reactions in cell narcosis.
5. Causes of volcanic eruptions.
6. The effects of past or present physical changes of the earth's surface on the development of species (*e. g.*, river work, changes of sea level, mountain building, etc.).

Two essays were received in competition, and a first prize of sixty dollars was awarded to Prof. George E. Stone, of Amherst, Mass., for his essay entitled "The influence of current electricity on plants"; a second prize of forty dollars was awarded to Dr. Burton E. Livingston, of Chicago, Ill., for the essay on "Ionic stimulation of algae."

The subjects announced for next year are: —

1. The life history of any parasitic fungus.
2. Contribution to our knowledge of the physiology of plants.
3. Contribution to the development of some group of fossil organisms.
4. Study of hybrids in animals or plants.
5. Critical study of geographical distribution of species.
6. A laboratory research in experimental geology.
7. A field study of the mechanism of baseleveling (peneplanation).
8. A research in mineral physics.
9. A contribution to geological correlation in the United States.

REPORT OF THE TREASURER, EDWARD T. BOUVÉ.

Annual Statement, May 4, 1904.

1903			1904		
May 1	To balance from April 30, 1903, belonging to		Apr. 30	By cash paid for	
	Library..... 1620.07			Fuel and Light.....	449.99
	Museum..... 950.00	2570.07		General Expense.....	1291.33
1904				Insurance..... 821.90	
Apr. 30	To cash received from income,			Less cash from Trustees 86.90	735.00
	General Fund.....	5373.28		Museum	1116.69
	Bulfinch Fund.....	1716.90		Library.....	2565.60
	Flint Fund.....	219.17		Publications.....	2099.54
	Pratt Fund.....	585.10		Salaries.....	7380.00
	Wolcott Fund.....	401.02		Walker Prize Adv.....	49.25
	Saltonstall Fund.....	1026.66		Janitor Services Lecture Hall renting.....	28.00
	Waterston Fund.....	454.96		Balance carried to new account	2095.31
	Walker Fund.....	1963.05		Of this there belongs to	
	Randall Fund.....	250.00		Library..... 224.49	
	Billings Fund.....	700.28		Museum 436.18	
	To cash from Mass. Inst. Technology.....	200.00		Publications 436.09	
	Admission Fees.....	135.00		General Expense 998.55	
	Annual Assessments.....	1515.10			
	Museum Fees.....	152.87			
	Sale of Publications.....	379.01			
	Rent of Lecture Hall.....	117.00			
	Int. on deposit in Shawmut Bank.....	51.24			
	Total,	$17,810.71		Total,	$17,810.71

TEACHERS' SCHOOL OF SCIENCE.

To cash received from A. L. Lowell, Trustee...	$2850.00	By cash paid for Lectures and Supplies	$2818.05
Interest on deposit Shawmut Bank.....	4.39	By balance to new account.....	36.34
Total,	$2854.39	Total,	$2854.39

ARMS FUND.

To balance from April 30, 1903..... ..	$1706.22	By balance to new account.....	$1740.34
Interest on deposit Shawmut Bank.....	34.12		
Total,	$1740.34	Total,	$1740.34

The report of the Trustees was presented, and the reports of the Auditing committee and of its expert accountant were read.

It was voted that these reports be accepted and placed on file. The Society then proceeded to the election of officers for the ensuing year. The Chair appointed Mr. J. Henry Blake and Mr. James H. Emerton to act as tellers. After the ballots had been collected and counted, it was announced that twenty-two ballots had been cast for each of the persons nominated, who were thus duly elected as follows: —

PRESIDENT,

CHARLES SEDGWICK MINOT.

VICE-PRESIDENTS,

CHARLES P. BOWDITCH. HENRY W. HAYNES.
ROLAND THAXTER

SECRETARY,

GLOVER M. ALLEN

TREASURER,

EDWARD T. BOUVÉ.

COUNCILLOR FOR TWO YEARS,

Miss Clara E. Cummings.

COUNCILLORS FOR THREE YEARS,

Frederic C. Bowditch.
James H. Emerton.
William A. Jeffries.
A. Lawrence Lowell.
Miss Susannah Minns.
Benjamin L. Robinson.
Theobald Smith.
Emile F. Williams.

OFFICERS FOR 1904-1905.

PRESIDENT,

CHARLES SEDGWICK MINOT.

VICE-PRESIDENTS,

CHARLES P. BOWDITCH. HENRY W. HAYNES.
ROLAND THAXTER.

CURATOR,

CHARLES W. JOHNSON.

SECRETARY,

GLOVER M. ALLEN.

TREASURER,

EDWARD T. BOUVÉ.

LIBRARIAN,

GLOVER M. ALLEN.

COUNCILLORS FOR THREE YEARS,

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James H. Emerton.
William A. Jeffries.
A. Lawrence Lowell.
Miss Susannah Minns.
Benjamin L. Robinson.
Theobald Smith.
Emile F. Williams.

COUNCILLORS FOR TWO YEARS,

Charles F. Batchelder.
Miss Clara E. Cummings.
William M. Davis.
Samuel Henshaw.
Nathaniel T. Kidder.
William H. Niles.
William L. Underwood.
Arthur W. Weysse.

COUNCILLORS FOR ONE YEAR,

Miss Cora H. Clarke.
Robert T. Jackson.
John S. Kingsley.
Edward S. Morse.
George H. Parker.
A. Lawrence Rotch.
William F. Whitney.
J. B. Woodworth.

COUNCILLORS *ex-officiis*,

George L. Goodale. Frederic W. Putnam.
Samuel H. Scudder.

Proceedings of the Boston Society of Natural History.

Vol. 32, No. 2,

p. 23–41, pl. 1.

LIST OF SHELL-BEARING MOLLUSCA OF FRENCHMAN'S BAY, MAINE.

By Dwight Blaney.

BOSTON:

PRINTED FOR THE SOCIETY.

November, 1904.

No. 2. — LIST OF SHELL-BEARING MOLLUSCA OF FRENCHMAN'S BAY, MAINE.

BY DWIGHT BLANEY.

The following one hundred and twenty-seven species and five varieties were collected during the summers of 1901, 1902, 1903, and 1904 by dredging and collecting on the shores. All species were found alive unless otherwise stated. Many species were also obtained by examination of the stomachs of haddock caught in the Bay. As many as thirty-eight species were found in one lot of ten stomachs in June, 1903.

The list has been arranged in the order given in Dall's Bulletin 37, U. S. national museum, and only such synonyms have been added as will suffice to identify the species to the student.

I am under obligation to Dr. W. H. Dall, Prof. A. E. Verrill, Miss Katherine J. Bush, Prof. Edward S. Morse, and Mr. C. W. Johnson for the identification of various species.

Pelecypoda.

LIBRARY
NEW YORK
BOTANICAL
GARDEN

Anomia simplex d'Orbigny.

Anomia ephippium, Gould, '**70**, p. 204.
Anomia electrica, Gould, '**70**, p. 205.
Anomia glabra, Verrill, '**73**, p. 696.

A few small specimens found inside dead shells of *Chrysodomus decemcostatus* Say.

Anomia aculeata Linné.

Found abundantly, attached to stones and shells, even on the brachiopod (*Terebratulina septentrionalis*), at all depths from 10 to 40 fathoms, hard bottom.

Pecten (Placopecten) magellanicus Gmelin.

Pecten tenuicostatus, Gould, '**70**, p. 196.
Chlamys (Placopecten) clintonius, Verrill, '**97**, p. 69.
Pecten (Placopecten) magellanicus, Dall, '**98**, p. 726.

Found commonly in colonies and of large size growing to over seven inches in diameter, 25 to 45 fathoms. Young specimens

dredged at station 17, full grown at station 11. This scallop is very good eating, and is much sought after by the natives. A. S. Packard ('67) in the Invertebrate fauna of Labrador, also mentions the edible quality of this species.

Pecten (Chlamys) islandicus (Müller).

Pecten islandicus, Gould, '**70**, p. 198.

Not found alive as yet by us, but abundant valves dredged at stations 10, 11, 17, 22,— 25 to 45 fathoms, hard bottom.

Mytilus edulis Linné.

Found most abundantly in colonies on rocks in many places about the Bay, covering large areas, as at Calf Island, the Narrows, etc. The natives report finding pearls in this species and also in *Modiolus modiolus* Linné. The so called variety *pellucidus* Pennant, is also found everywhere with the *edulis* though it is not so numerous.

Modiolus modiolus (Linné).

Modiola modiolus, Gould, '**70**, p. 186.
Modiolus modiolus, Dall, '**98**, p. 790.

Found abundantly on hard bottom at all depths, also in tide pools firmly wedged in crevices. Used by fishermen as bait; grows to large size in deep water and is often brought up on trawls.

Modiolaria nigra (Gray).

Not common, dredged at station 9 — muddy bottom — though a few were dredged at station 23 on rather hard bottom. The young specimens are a chestnut brown color, becoming black in the adult.

Modiolaria corrugata Gould.

Not common, dredged at stations 6 and 12, hard bottom. A few found in haddock, June 7, 1903.

Modiolaria discors (Linné).

Common, usually found imbedded in branches of seaweed or around roots of Laminaria. Stations 17 and 23, hard bottom.

Crenella glandula (Totten).

Abundant on muddy bottoms, 10 to 20 fathoms, stations 1, 2, 7, 9, 13.

Crenella decussata (Montagu).

Found abundantly with the preceding species — same conditions.

Nucula tenuis (Montagu).

Common, dredged abundantly at stations 7, 8, 9, muddy bottom, 10 to 20 fathoms; also found abundant in haddock.

Nucula proxima Say.

Most abundant, everywhere on muddy bottom. Found in haddock, some fish having only this species in large numbers in stomach.

Nucula delphinodonta Mighels.

Very common, found usually in company with the preceding, as also in haddock.

Yoldia limatula (Say).

Rather rare, found occasionally in haddock; a few valves of large size dredged in Calf Island Bay. Found common and of large size in Somes Sound, Mount Desert Island, by Mr. Harold S. Colton. We have dug a rich yellow colored form from mud off Soward's Island, at just below low water mark, during low spring tides. Some specimens were over two inches in length.

Yoldia sapotilla (Gould).

Very common, dredged in large numbers on soft bottom at stations 1, 2, 7, 9, 10, 12, in 15 to 35 fathoms. Also found common in haddock. Specimens dredged at station 13 ovulating on August 21st. The eggs were of a delicate pink tint.

Yoldia myalis (Couthouy).

A few specimens dredged near station 18.

Yoldia thraciaeformis (Storer).

A few found of large size in sticky mud at station 9. Young specimens very common in August at station 12. Many young found in haddock.

Leda tenuisulcata (Couthouy).

Not common, dredged at stations 3, 7, 8, 10, rather muddy bottom. Also found in haddock.

Venericardia (Cyclocardia) borealis (Conrad).

Cardita borealis, Gould, '**70**, p. 146.

Abundant, large specimens dredged on hard bottom at stations 7, 8, 9, 10. The adult specimens were much more elevated in shape than the young.

Venericardia (Cyclocardia) novangliae (Morse).

Cyclocardia novangliae Morse, '**69**, p. 76.

Not as common as the preceding with which it is found and from which it is readily distinguished by its much finer sculpture and character of hinge margins.

Astarte castanea (Say).

Rather rare, a few specimens dredged at station 17.

Astarte undata Gould.

Astarte sulcata, Gould (not DaCosta), '**70**, p. 119.
Astarte undata Gould, '**70**, p. 121.

Very common, though of small size, at station 7. Full grown specimens common in deeper water at station 17. Quantities of dead shells of large size at station 11.

Astarte undata var. **latisulca** (Hanley).

Astarte undata var. *latisulca*, Dall, :**03**, p. 938.

Common with the preceding.

Astarte subaequilatera Sowerby.

Astarte crebricostata, Gould, '**70**, p. 126.
Astarte lens, Dall, :**03**, p. 939.

Rather common, hard bottom, stations 17, 22.

Astarte borealis Schumacher.

Astarte semisulcata, Gould, '**70**, p. 121.

Rare, only valves dredged at station 17.

Note. — This and the following species are placed in section Tridonta Schum. by Dall. This species is the type.

Astarte banksii Leach.

Rare, only valves dredged, station 24. This is an Arctic American species.

Turtonia minuta (Fabricius).

A few found in crevices of piles between tides. Also found abundant in mud about stones, on rough beaches between tides.

Thyasira gouldii (Philippi).

Cryptodon gouldii, Gould, '**70**, p. 100.

Very abundant on rather soft bottom, 20 to 40 fathoms. Found in haddock.

Thyasira plana (Verrill and Bush).

Cryptodon planus Verrill and Bush, '**98**, p. 788.

A few of this species were identified by Professor Verrill and Miss Bush from among a number of *T. gouldii* sent to the Yale museum.

Axinopsis orbiculata Sars.

Rare; a few dredged 100 yards west of Ryefield Point, Ironbound Island, in 1904, at 15 fathoms.

Axinopsis orbiculata var. **inequalis** Verrill and Bush.

Rare; dredged in same locality as above.

Cardium (**Cerastoderma**) **pinnulatum** Conrad.

Very common, found almost everywhere, 20 to 30 fathoms. The largest specimens in haddock.

Cardium (**Cerastoderma**) **ciliatum** Fabricius.

Cardium islandicum, Gould, '**70**, p. 139.

Not rare, dredged at stations 10, 17, 18, and 22, on hard bottom, 20 to 30 fathoms. All specimens, even large ones, with the epidermis.

Serripes groenlandicus (Gmelin).

Aphrodite groenlandica, Gould, '**70**, p. 144.

A few large valves dredged at station 6, and a few young live specimens with the pretty red zig-zag markings dredged at station 7.

Cyclas islandica (Linné).

Cyprina islandica, Gould, '**70**, p. 129.

Common though of small size at station 7. Full grown specimens dredged by Mr. H. S. Colton at Southwest Harbor, Mt. Desert.

Venus mercenaria Linné.

One valve dredged at station 4.

Gemma gemma (Totten).

Gemma gemma, Dall, : **02a**, p. 378.

One valve of this small species, still tinted with purple, dredged off western shore of Ironbound Island, 150 yards west of Ryefield Point, 15 fathoms, mud and gravel.

Liocyma fluctuosa (Gould).

Tapes fluctuosa, Gould, '**70**, p. 136.
Lyocyma fluctuosa, Dall, : **02a**, p. 378.

Rare, a few valves dredged at station 10.

Macoma balthica (Linné).

Macoma fusca, Gould, '**70**, p. 94.
Macoma balthica, Dall, : **00**, p. 298.

Very abundant in shallow water. The shells vary greatly in solidity, some being thin and tinged with pink or yellow.

Macoma calcarea (Gmelin).

Macoma proxima, Gould, '**70**, p. 95.
Macoma calcarea, Dall, : **00**, p. 299.

Common, dredged in 10 to 15 fathoms, stations 1, 2, 4, 8, and 13

Spisula (Hemimactra) polynyma (Stimpson).

Mactra ovalis, Gould, '**70**, p. 75.

Only valves dredged as yet, station 18, though it is reported alive on Stave Island bar.

Thracia conradi Couthouy.

Rare, valves of large size dredged at stations 6 and 16. Young alive, small, station 7.

Thracia myopsis Beck.

Frequent, dredged at stations 2, 4, 12.

Thracia truncata Mighels and Adams.

Frequent, only valves dredged, stations 22, 24, and 27.

Periploma fragilis (Totten).

Anatina papyracea, Gould, '**70**, p. 66.

Frequent, dredged at stations 4, 12, and 13. Also found in haddock.

Lyonsia hyalina (Conrad).

Common, dredged at stations 1, 2, and 4.

Lyonsia arenosa (Möller.)

Rare, only one specimen, dredged at station 2.

Cuspidaria sp.

One defective specimen, dead. Suggested by Dr. W. H. Dall as probably the *C. glacialis* Sars, '**78**, p. 88, pl. 6, fig. 8. Dredged 100 yards south of Egg Rock light, 25 fathoms, mud and gravel.

Pandora (Clidiophora) gouldiana Dall.

Pandora trilineata Gould, (not Say), '**70**, p. 62.
Pandora (*Clidiophora*) *gouldiana* Dall, :**02**, p. 511.

Only valves dredged by us at stations 22 and 23. It is probably found alive in shallow water up the Bay. Found alive and common by Mr. H. S. Colton at Southwest Harbor, Mt. Desert.

Mya arenaria Linné.

Abundant, found in large colonies in many places about the Bay, as at Stave Island Harbor, and Yellow Island, etc., also on Ironbound Island on the northeast shore among the rocks, where very distorted specimens were found. The young dredged in deep water, 20 to 40 fathoms, are quite different in shape from those grown in soft mud, and have angulated form. Immense deposits of shells in the many Indian shellheaps about the Bay.

Mya truncata Linné.

Only valves dredged at stations 17, 19, 22, deep water. They show great variation.

Panomya norvegica (Spengler).

Panopaea arctica, Gould, '**70**, p. 51.
Panomya norvegica, Dall, '**98**, p. 832.

Only valves of this interesting arctic species found at stations 17,

22. Verrill ('74) reports dredging it in 115 fathoms off Casco Bay, Maine, in 1873.

Saxicava arctica (Linné).

Saxicava rugosa, Gould, '70, p. 87.

Very abundant, wedged in rock crevices in tide pools. Very large specimens found in pool on Yellow Island.

Cyrtodaria siliqua (Daudin).

Glycimeris siliqua, Gould, '70, p. 53.
Cyrtodaria siliqua, Dall, '98, p. 835.

Rare, only valves dredged, station 14.

Ensis directus (Conrad).

Solen directus, Conrad, '43, p. 325.
Solen ensis Linné, var. *americanus* Gould, '70, p. 42.
Ensis directus, Dall, '99a, p. 108.

Common in colonies in a few places about the Bay, as in Hammond's Cove, just below low water. Called "razor fish" by the natives.

Zirfaea crispata (Linné).

One valve about $\frac{1}{2}$ inch in length in dredgings off Yellow Island, Aug., 1904, 10 fathoms, muddy.

Teredo megotara Hanley.

Many specimens found in a piece of driftwood cast up on the beach in Jacob's Cove, Ironbound Island, after a hard southerly storm, Sept. 10, 1902. We also found specimens of the *Lepas anatifera* and *L. pectinata* attached to wood at the same time.

Scaphopoda.

Dentalium entalis (Linné).

Entalis striolata, Gould, '70, p. 266.
Dentalium entalis, Pilsbry, '97, p. 42.

Very common in a few places, as at stations 17 and 22.

Dentalium occidentale Stimpson.

Dentalium dentale, Gould, '70, p. 266.

A few specimens, dead, dredged at station 4.

GASTROPODA.

Retusa gouldii (Couthouy).

Utriculus gouldii, Gould, '**70**, p. 217.
Cylichna gouldii, Verrill, '**81**, p. 383.
Retusa gouldii, Pilsbry, '**93**, p. 217.

Rare, a few found in company with the following species.

NOTE.— Formerly in Utriculus, now in subgenus.

Retusa pertenuis (Mighels).

Utriculus pertenuis, Gould, '**70**, p. 218.
Retusa pertenuis, Pilsbry, '**93**, p. 216.

Very common, dredged at stations 12 and 13.

Cylichna alba (Brown).

Very common, dredged at stations from 10 to 30 fathoms, mud, sand, and gravel; Flander's Bay, Stave Island Bay, etc. The largest specimens off Ironbound Island, station 17.

Amphisphyra pellucida (Brown).

Diaphana debilis, Gould, '**70**, p. 216.
Amphisphyra pellucida, Verrill, '**81**, p. 382.

Uncommon, dredged at stations 7 and 12. The best specimens dredged in Calf Island Bay.

Bela incisula Verrill.

Bela impressa Verrill (not Mörch), '**81**, p. 365.
Bela incisula Verrill, '**82**, p. 461.

This is the most common of the Belas found in the Bay. We have dredged it on almost all kinds of bottom from soft to hard. Abundant at stations 1, 4, 7, 8, and 10.

Bela gouldii Verrill.

Bela virgulata Verrill (not Reeve), '**81**, p. 365.
Bela gouldii Verrill, '**82**, p. 465.

Only one dead specimen dredged at station 17.

Bela mitrula (Lovén).

Bela mitrula, Verrill, '**84**, p. 249.

Rare, dredged at stations 1 and 2.

Bela mitrula var. **concinnula** (Verrill).

Bela concinnula Verrill, '**82**, p. 468.
Bela exarata Verrill (pars), '**82**, p. 467.
Bela mitrula var. *concinnula* Verrill, '**84**, p. 266.

Rather rare, dredged at stations 2 and 4.

Bela nobilis (Möller).

Defrancia nobilis Möller, '**42**, p. 85.
Bela scalaris, Verrill, '**82**, p. 471.
Bela turricula, Gould (not Montagu), '**70**, p. 351.

Very common at many stations, as stations 4, 7, 10, 11, and 17. The typical *B. scalaris* has a more acute spire and larger canal than this species.

Bela harpularia (Couthouy).

Rather common, dredged at stations 8, 10, and 11.

Bela cancellata (Mighels and Adams).

A few specimens dredged $\frac{1}{2}$ mile south of Egg Rock light, 25 fathoms, rocky. They were the slender form.

Bela pleurotomaria (Couthouy).

Not rare, dredged at stations 4, 10, and 11.

Bela decussata (Couthouy).

Rather rare, dredged at stations 1, 2, and 4.

Bela bicarinata (Couthouy).

Pleurotoma bicarinata, Gould, '**70**, p. 349.
Bela bicarinata, Verrill, '**82**, p. 481.

Rare, dredged at station 10.

Bela bicarinata var. **violacea** (Mighels and Adams).

Bela violacea, Gould, '**70**, p. 353.
Bela bicarinata var. *violacea*, Verrill, '**82**, p. 483.

Not rare, dredged at stations 4, 8, and 10.

Admete couthouyi (Jay).

Admete viridula, Gould, '**70**, p. 391.

Rare, a few dredged at station 17. Also a few found in haddock.

Buccinum undatum Linné.

Very abundant; in tide pools, also dredged in shallow water on hard bottom in many places.

Buccinum cyaneum (Bruguière).

Buccinum grönlandicum, G. O. Sars. '**78**, p. 259.
Buccinum cyaneum, Verrill, '**82**, p. 492.

One immature specimen, with protoconch, dredged, 10 fathoms, station 16, Sept. 1, 1902.

Chrysodomus decemcostatus (Say).

Fusus decemcostatus, Gould, '**70**, p. 375.

Very common, dredged in many places about the Bay, usually hard bottom. Fine large specimens of this and the following species were taken by baiting a net with refuse fish and sinking over night at station 15.

Sipho stimpsoni Mörch.

Fusus islandicus, Gould (not Linné), '**70**, p. 371.

Very common on hard bottom near shore, very rarely dredged fully grown as it lives on such rough bottom.

Sipho pygmaeus (Stimpson).

Fusus pygmaeus, Gould, '**70**, p. 372.

Very common, dredged almost everywhere on hard bottom.

Nassa (Tritia) trivittata Say.

Nassa trivittata. Gould, '**70**, p. 364.

Very abundant; found everywhere on soft bottom. Does not grow to such large size as farther south.

Columbella (Astyris) rosacea (Gould).

Columbella rosacea, Gould, '**70**, p. 357.

Not rare, dredged at stations 6, 8, and 10.

Trophon clathratus (Linné).

Not rare, dredged at stations 10 and 11. Our specimens agree perfectly with the drawing given by Sars ('**78**) as *Trophon truncatus* Strom.

Purpura lapillus (Linné).

Most abundant on the outer rocks everywhere. A most variable species; series from different islands show great variations in size, color, and proportion. The sharply ridged form, *P. imbricata* of Lamarck, is found in the tide pools on Shag Point at Ironbound Island; and at Yellow Island a bright yellow form predominates over the duller colored individuals. The yellowish and reddish rocks give the name to the island. In sheltered places it grows to large size. We have found specimens $1\frac{3}{4}$ inches long.

Scala groenlandica (Perry).

Scalaria groenlandica, Gould, '**70**, p. 314.

Rather common at stations 4, 8, 10, and 17. Portions of the live animal on removal from the shell are of a most beautiful purple color. The shells here are pure white and the operculum black.

Turbonilla sp.

Only one dead and very worn specimen found which suggests "*Turbonilla nivea*" Stimpson, dredged at station 24.

Menestho albula Möller.

Rather common, dredged at stations 17, 19, and 22.

Odostomia modesta (Stimpson).

Rare, a few dredged at station 6.

Odostomia producta (Adams).

Only one dead and worn specimen dredged at station 6.

Trichotropis borealis Sowerby.

Common at stations 10, 11, and 17.

Mesalia acicula (Stimpson).

Turritella acicula, Gould, '**70**, p. 319.

Not rare though of small size. Dredged at stations 5 and 12.

Mesalia erosa (Couthouy).

Turritella erosa, Gould, '**70**, p. 317.

Rare, only one dead and eroded specimen, dredged at station 21, but fine large live specimens dredged in 15 fathoms, mud, 500 yards south of Egg Rock light.

Litorina littorea (Linné).

Littorina litorea, Gould, '**70**, p. 308.

Very abundant on rocky shores between tides, growing very large in favorable localities. Specimens found $1\frac{3}{8}$ inches long.

Litorina rudis (Donovan).

Littorina tenebrosa, Gould, '**70**, p. 306.

Very abundant with the preceding; shows considerable variation in coloring.

Litorina palliata (Say).

Very abundant with the preceding.

Lacuna vincta (Montagu).

Found abundantly on Laminaria.

Jeffreysia eburnea (Stimpson).

Rissoella? eburnea, Gould, '**70**, p. 297.

Not rare, dredged at station 6.

Cingula minuta (Totten).

Rissoa minuta, Gould, '**70**, p. 298.

A few dredged in Calf Island Bay in shallow water, muddy bottom, also station 12.

Cingula aculeus Gould.

Rissoa aculeus, Gould, '**70**, p. 299.

Very common in tide pools, under stones.

Cingula castanea (Möller).

Rissoa castanea Möller, '**42**–'**43**, p. 82.
Cingula castanea Sars, '**78**, p. 174, pl. 10, figs. 1a, 1b.

Not rare, dredged at stations 1, 2, and 6.

Cingula carinata Mighels and Adams.

Very abundant in 15 fathoms at station 6, in sandy mud. This is the only place where we have dredged this species.

Cingula arenaria Mighels and Adams.

Rissoa mighelsii, Gould, '**70**, p. 301.
Rissoa exarata, Gould, '**70**, p 301.

Common at station 6.

Cingula areolata (Stimpson).

Turritella areolata Stimpson, '**51**, p. 35.
Cingula areolata Verrill, '**82**, p. 524.

Not common, found with the preceding.

Cingula multilineata (Stimpson).

Rissoa multilineata, Gould, '**70**, p. 300.

Only one dead specimen, dredged at station 5.

Aporrhais occidentalis (Beck).

Rare, dead specimens and fragments dredged at stations 4 and 10. Dredged alive in sandy mud, May, 1904, between stations 4 and 6, 15 fathoms. No specimens fully matured, all being without lip. The animals seemed very hardy, as they were kept alive for study for three weeks. One live specimen, full grown, dredged 500 yards south of Egg Rock light, in August, 1904.

Skenea planorbis (Fabricius).

Very common in tide pools.

Crucibulum striatum (Say).

Not rare, dredged at stations 3, 4, and 6, attached to stones.

Natica clausa Broderip and Sowerby.

Rather rare, dredged at stations 17 and 22.

Lunatia heros (Say).

Common in shallow water, muddy bottom, in the upper part of Bay, as off Soward's Island, and Shelldrake Island in Flander's Bay, Called "hoss winkles" by the natives!

Lunatia heros var. **triseriata** (Say).

Lunatia triseriata, Gould, '**70**, p. 340.

Very common; in deeper water than the preceding. Dredged about everywhere in the Bay.

Lunatia groenlandica (Möller).

Rare, a few specimens dredged at station 10.

Lunatia immaculata (Totten).

Mamma ? immaculata, Gould, '**70**, p. 344.

Very common, dredged at stations 10, 11, 17, and 22.

Velutina laevigata (Linné).

Velutina haliotoidea, Gould, '**70**, p. 334.

Very common, dredged at stations 4, 10, 11, and 17.

Velutina zonata Gould.

Only one dead specimen dredged at station 17. Five fresh specimens found in haddock.

Marsenina glabra (Couthouy).

Lamellaria perspicua, Gould, '**70**, p. 337.

Only one dead specimen dredged at station 22.

Acmaea testudinalis (Müller).

Tectura testudinalis, Gould, '**70**, p. 267.

Very abundant on rocks between tides everywhere. Grows to over 1½ inches long in favorable localities.

Acmaea alveus (Conrad).

Tectura alveus, Gould, '**70**, p. 269.

Acmaea testudinalis var. *alveus*, Pilsbry, '**91**, p. 11.

A few found under beach stones; reported common on eel grass.

Lepeta caeca (Müller).

Common at stations 17 and 22 only. Live specimens attached to stones and dead shells.

Calliostoma occidentalis (Mighels and Adams).

Trochus occidentalis, Gould, '**70**, p. 286.

Only one broken specimen taken from haddock.

Solariella obscura (Couthouy).

Margarita obscura, Gould, '**70**, p. 283.

Machaeroplax obscura, Verrill, '**82**, p. 531.

Rather common, dredged on hard bottom at stations 4, 6, 10, and 23. A few specimens of a two-keeled form have also been dredged with the typical specimens.

Margarita helicina (Phippe).

Turbo helicina Phippe, Voyage toward the north pole, **1774**, p. 198.

Not rare, found in tide pools and under beach stones at low tide mark. Also dredged on Laminaria at station 16. The *Margarita campanulata* Morse, first described in Packard's Invertebrate fauna of Labrador ('67) is now held by Morse, himself, to be the male of the *M. helicina*. There is considerable difference between sexes in the shape, and 75 percent of the specimens found are males.

Margarita groenlandica (Gmelin).

Margarita undulata, Gould, '70, p. 280.

Rather common, in company with the *M. obscura*.

Margarita cinerea (Couthouy).

Rather common with the preceding at stations 4, 6, 17, and 20. A few found in haddock.

Margarita argentata Gould.

Rare, a few dredged at station 17. Most of the specimens taken from haddock.

Molleria costulata (Möller).

Adeorbis costulata, Gould, '70, p. 278.

Common at station 17. Also dredged dead at stations 22 and 24 among broken shells.

Puncturella noachina (Linné).

Cemoria noachina, Gould, '70, p. 276.

Very common; at stations 17 and 22 attached to stones and dead shells. A few specimens dredged with the others resemble the much elevated form described by Mighels as *Cemoria princeps*.

Polyplacophora.

Hanleyia mendicaria (Mighels and Adams).

Chiton mendicarius, Gould, '70, p. 263.

Rare. This is a deep water species, though Professor Verrill ('74) in Explorations of Casco Bay, 1873, records specimens dredged in 30 fathoms. Only one specimen dredged at station 17, in 25 to 30 fathoms.

Trachydermon ruber (Linné).

Chiton ruber, Gould, '**70**, p. 260.

Very common; in tide pools and dredged on hard bottom to 50 fathoms. One abnormal specimen of this species having only six valves was found in 1902 in a tide pool at Shag Point, Ironbound Island. This is of very rare occurrence. The only other six-valved specimen I can find recorded was from California and is mentioned in vol. 15, no. 5, p. 53, of the "Nautilus."

Trachydermon albus (Linné).

Chiton albus, Gould, '**70**, p. 263.

Common, dredged at stations 4 and 6, hard bottom. Also found in haddock.

Tonicella marmorea (Fabricius).

Chiton marmoreus, Gould, '**70**, p. 261.

Common in tide pools and dredged at stations 10 and 11. Not found over half an inch long.

Amicula vestita (Broderip and Sowerby).

Amicula emersonii, Gould, '**70**, p. 264.
Amicula vestita, Pilsbry, '**93**, p. 43.

Only one specimen, taken from a haddock.

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Printed November, 1904.

EXPLANATION OF PLATE.

The depth of water and character of bottom of the twenty-four stations shown on the map are as follows.

(Note.— These represent exactly 100 hauls of the dredge.)

Station 1. } Between these two stations the depth was from 10 to 12 fathoms —
" 2. } soft, with gravel.

" 3. 10 to 12 fathoms — hard. This is the dumping ground for Bar Harbor refuse.

" 4. 10 fathoms — hard.

" 5. 5 " — rocky in channel, becoming fine black sand nearer shore.

" 6. 6 to 8 fathoms — hard.

" 7. 16 fathoms — soft, with occasional rocks.

" 8. 15 " — hard.

" 9. 28 " — very soft sticky mud.

" 10. 35 " — hard, though with occasional patches of mud and gravel.

" 11. 40 to 50 fathoms — hard, with worn lumps of hard green clay.

" 12. 10 fathoms — soft, with gravel.

" 13. 4 to 6 fathoms — soft.

" 14. 5 fathoms — all broken shells.

" 15. 10 " — hard, rocky.

" 16. 5 to 10 fathoms — hard.

" 17. 25 to 30 " — " (Brachiopods at this station.)

" 18. 10 to 15 " — hard and rocky.

" 19. 20 fathoms — hard.

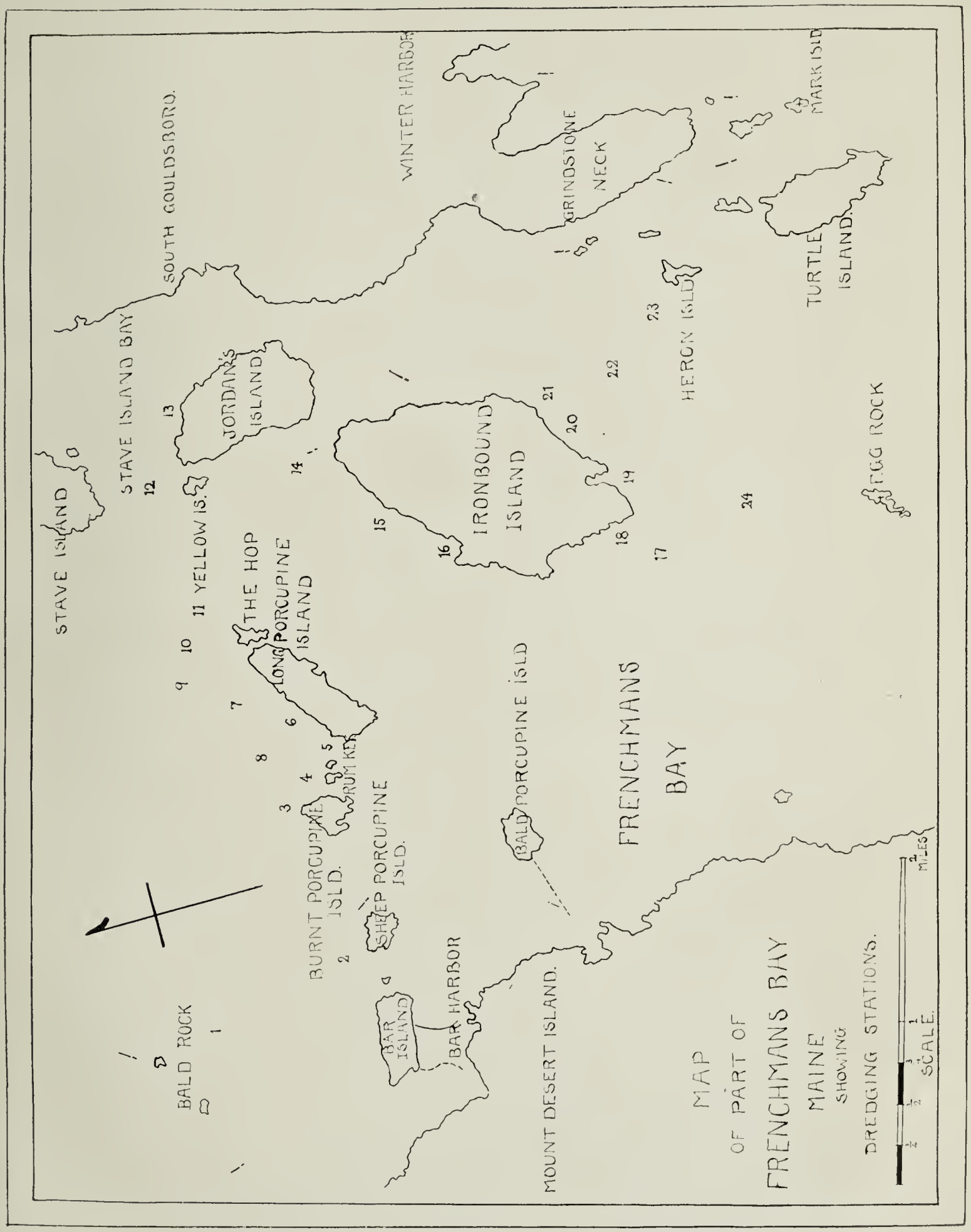
" 20. 15 to 20 fathoms — hard and rocky.

" 21. 7 fathoms — hard, with patches of broken shells.

" 22. 25 " — " (Brachiopods at this station.)

" 23. 15 to 20 fathoms — hard.

" 24. 20 fathoms — mud and broken shells.


STAVE ISLAND
STAVE ISLAND BAY
SOUTH GOULDSBORO.
WINTER HARBOR
GRINDSTONE NECK
MARK ISLD
TURTLE ISLAND.
EGG ROCK
HERON ISLD
IRONBOUND ISLAND
JORDAN'S ISLAND
YELLOW IS.
THE HOP
PORCUPINE ISLAND
LONG PORCUPINE ISLAND
RUM KEY
BURNT PORCUPINE ISLD.
SHEEP PORCUPINE ISLD.
BAR ISLAND
BAR HARBOR
BALD ROCK
BALD PORCUPINE ISLD
MOUNT DESERT ISLAND.
FRENCHMANS BAY
MAP
OF PART OF
FRENCHMANS BAY
MAINE
SHOWING
DREDGING STATIONS.
SCALE.
MILES

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GENERAL ANATOMY OF *TYPHLOMOLGE RATHBUNI.*

By Ellen Tucker Emerson, 2d.

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No. 3.—GENERAL ANATOMY OF *TYPHLOMOLGE RATHBUNI.*[1]

BY ELLEN TUCKER EMERSON, 2d.

Introduction.

Typhlomolge rathbuni Stejneger, a blind, cave salamander, was discovered in 1894, when a dozen or more specimens were thrown up from an artesian well 188 feet deep, which had been bored by the United States fish commission, at San Marcos, Texas. An announcement of this discovery and a brief description of the animal, from which I quote, were given by Dr. Leonhard Stejneger ('96).

"*Description of type specimen.*— Head excessively large and broad, the distance from tip of snout to base of upper gill branch but slightly less than distance between axilla and groin, its width equal to one-half the latter distance; snout very much depressed, broad, truncated, nearly square anteriorly; nostrils widely separated at the corners of the truncated snout, their distance greater than that between the eyes, which are deeply hidden under the skin and only visible as two small dark spots; mouth comparatively small, with strongly developed labial lobes; body short and slender, the distance between axilla and groin being but slightly greater than length of head and only one-half the length of the tail, its width being much less than that of the head and even less than that of the snout; limbs excessively slender and long, of nearly even length, about one-fifth of the total length; fingers overlapping knee and toes overlapping elbow when adpressed to the sides of the body; fingers four, toes five; short, slender, free, with rounded tips, their relative length variable; tail comparatively long, nearly one-half the total length, much compressed, finned below and particularly strongly above, the end pointed.

Skin smooth; a very strongly marked gular fold; a well marked vertebral groove; eleven costal grooves. Teeth on intermaxillaries and mandible small; the vomero-palatine teeth large, decreasing in size at both ends. Gill branches long and slender, the middle one longer; fimbriae long and slender, not bushy.

[1] Thesis prepared under the Fellowship in zoology, Smith college.

Color nearly white, semitransparent, the upper surface densely sprinkled with minute pale gray dots."

The most striking characteristics of those here mentioned are the small, functionless, subcutaneous eyes, the white, slightly iridescent skin, reminding one of the integument of Proteus, the extreme length and slenderness of the limbs and the great size of the head as compared with that of the body. The first two make it evident at first sight that the animals are cave dwellers, but to quote again from Stejneger, "their extraordinary proportions, absolutely unique in the order to which they belong, suggest unusual conditions of life, which alone can have produced such profound differences."

Before giving this description, Stejneger says that he intends "later to present, in conjunction with Mr. F. A. Lucas, a detailed description of the anatomy and an elaborate comparison with allied forms," but as eight years have elapsed since the preliminary description was published, it may not seem discourteous to presume that the idea has been given up.

In addition to the external characteristics given above, I should mention that there are three gill slits present in Typhlomolge: one between the hyoid and the first branchial arch, one between the first and second branchial arches, and one between the second and third branchial arches. The external gills persist even in the sexually mature animals, a fact which, "in conjunction with the affinity of the species to other forms known to have persistent gills throughout life, makes it absolutely certain that we have to do with an adult and final animal" (Stejneger). In view of these external characteristics and after a brief study of a rough skeleton, Stejneger classifies Typhlomolge as belonging to the superfamily Proteoideae, which embraces Proteus and Necturus, but after careful examination of two specimens of Typhlomolge and comparison of them with various other Urodelous forms, I am of the opinion that this view must be changed.

The two specimens which I had for study were preserved in four percent formalin and were in very good condition for dissection and sectioning, although they were not very satisfactory for histological work. The smaller of the specimens had been partially dissected in the hyoid region and one of the fore limbs had been removed before it came into my hands. It was therefore impossible to make out certain details. The small specimen was used for the study of

bones and muscles, and the body of the larger one was studied for the viscera and to some extent for the vertebrae, while the head of this specimen was used for serial cross-sections.

The following table gives measurements of the two specimens and of the specimen described by Stejneger: —

	Specimen 1.	Specimen 2.	Stejneger's specimen.
Total length	86 mm.	81 mm.	102 mm.
Snout to anus	48 "	45.5 "	53 "
Snout to gular fold	13 "	—	16 "
Width of head	10.5 "	9.5 "	13 "
Length of fore limb	18 "	16.5 "	20 "
Length of hind limb	18 "	15.5 "	20 "

I wish to take this opportunity to express my gratitude to Dr. H. H. Wilder, under whose direction this work has been done, for his constant advice and helpful criticism. My thanks are also due to the Hon. George M. Bowers, of the United States fish commission, through whose courtesy Dr. Wilder obtained the two specimens I had for study.

Axial Skeleton.

The Skull.

The skull of Typhlomolge is in shape an elongated hexagon, with the longitudinal axis about twice as long as the transverse. The anterior side of this figure is formed by the premaxillary, the antero-lateral sides by the ligaments between the premaxillary and the quadrates, the postero-lateral sides by the paraquadrates and periotics, and the posterior side by the periotics and occipitals.

From a dorsal aspect the chondrocranium is not visible with the exception of the ante-orbital processes, the trabeculo-quadrate isthmus, and the supra-occipital arch. The conspicuous bones which cover it are the premaxillary, the frontals and parietals, and the periotics. The paraquadrates are also prominent features. All these bones are thin and quite transparent, so that the brain and many of the cranial nerves show through, but this transparency renders it hard to make out the extent of the individual bones.

From the ventral aspect the most conspicuous feature is the large flat parabasal, from which project anteriorly and laterally the dentigerous premaxillary, vomers, and palato-pterygoids. Posteriorly the periotics and paraquadrates are prominent. Of the primordial skull the posterior portion of the trabeculae, the trabeculo-quadrate isthmus, the flattened portion of the rods anterior to the ante-orbital process, and the basi-occipital arch are visible.

Only one skull was available for dissection and the bones of this proved to be extremely difficult to separate. It was kept in a three percent solution of caustic potash for several days with no effect, then put into a ten percent solution for several days more, but even after this it was impossible to separate the bones, especially the frontals and parietals, without injuring them. The material was so far from satisfactory that I shall not attempt to give a detailed description of the separate bones. The description given has been carefully corroborated by study of the cross sections of the head of the second specimen.

Chondrocranium.

The greater part of the chondrocranium consists of two rods lying nearly parallel to each another. Anteriorly these are flattened and connected by a small isthmus and are covered by the posterior two thirds of the premaxillary. Between this region and the eyes, the rods are cylindrical, each having on its lateral border a flattened triangular process which protrudes laterally from under the edge of the frontal, the ante-orbital process.

In the trabecular region, the rods are very slender but their dorso-ventral axis elongates. They diverge slightly and form the sides of the brain case. Posterior to this portion, each rod is connected laterally with the quadrate cartilage by a broad, flattened, cartilaginous process, the trabeculo-quadrate isthmus. Posteriorly the rods articulate with small notches in the parabasal and with the anterior border of the otic capsule.

The parachordal region of the chondrocranium is so closely connected with the bony parts of the otic and occipital region as to be indistinguishable from them. The supra-occipital arch appears as a short and narrow cartilaginous bridge between the middle thirds of the bony periotics. It is also contiguous to the parietals in the

angle made by their divergent posterior processes. The position of the supra-occipital here is identical with its position in the larva of *Spelerpes ruber* and very similar to its position in *Triton alpestris* as shown by Wiedersheim ('**77**, pl. 6, fig. 83). In Necturus this supra-occipital arch is confluent with the cartilaginous otic capsules.

The basi-occipital arch is also present. Anteriorly it appears as a flat bit of cartilage on the dorsal surface of the posterior end of the parabasal, connecting the ventral surface of the periotics. It becomes broader, and posterior to the parabasal narrows again, its dorsal surface having a median longitudinal depression. Here the median process of the first vertebra lies dorsal to it and is contiguous to it laterally.

The basi-occipital in Typhlomolge is identical in shape and position with that of the Spelerpes larva and corresponds closely with that of *Triton alpestris* (Wiedersheim, '**77**, pl. 6, fig. 83). The arrangement of both basi- and supra-occipital arches in the Proteidae is quite different.

Another characteristic of the chondrocranium common to Typhlomolge and Spelerpes larva is the entire lack of bony or cartilaginous nasal capsules. In the Proteidae the capsules are large and cartilaginous.

Osseous Elements.

The otic and occipital region. — In the otic and occipital region the skull of Typhlomolge differs markedly from that of the Proteidae and resembles that of the larva of Spelerpes closely. While in Necturus and Proteus the osseous elements, exoccipitals, periotics, and opisthotics are quite distinct and separate, embedded in the cartilage of the parachordal region of the chondrocranium, in Typhlomolge, as in Spelerpes, these elements are not differentiated but are fused with the parachordal region of the chondrocranium into two oval bony masses, the periotics or otic capsules, on which the configuration of the semicircular canals is very plain. Stejneger makes out "the presence of what appears to be an intercalary bone." If, as seems probable, he follows Cope's nomenclature and uses "intercalary" for "opisthotic," he is mistaken, for the opisthotic *as such* does not exist in this form.

The anterior portion of the periotic, corresponding to the pro-otic

of certain other forms, is overlapped dorsally by the parietals and ventrally by the parabasal. The middle portions of the periotics are contiguous in the mid-dorsal region with the supra-occipital cartilage, and posterior to this they diverge, forming two processes, the occipital condyles, thus suggesting the probable incorporation into this region of the exoccipital elements.

On the outer edge of the ventral surface of each periotic is the large fenestra ovalis into which the large oval operculum fits. On its antero-lateral border, the periotic is overlapped by the paraquadrate, while the trabeculo-quadrate isthmus and the posterior end of the trabecula are contignous to its anterior border. The inner edges of the periotics are connected posteriorly by the basi-occipital cartilage, which they partially invest laterally.

The quadrate or suspensorium consists of a broad, flat, bony head articulating with the rounded end of Meckel's cartilage, and a tapering cartilaginous neck which is closely wrapped by the anterior portion of the paraquadrate.

The mandible and hyoid apparatus are firmly held in place by three ligaments: the ligamentum hyo-suspensoriale, from the inner anterior portion of the neck of the quadrate to the distal end of the hyoid; the ligamentum mandibulo-hyoideum internum, from this latter point to the postero-ventral angle of the angulare; and the ligamentum mandibulo-hyoideum externum, to this latter point from a point on the anterior edge of the hyoid some distance below the attachment of the other ligaments. A membrane extending from the skull to the distal end of the hyoid is also present, arising partly from the operculum. It thus resembles the condition in Necturus as described by H. H. Wilder (:03) rather than the condition which Huxley ('74) describes in that animal.

The paraquadrate is a thin bony plate, convex on its outer surface and deeply grooved on its inner surface. In the anterior portion of this groove lies the quadrate, while the posterior part is in contact with the antero-lateral portion of the otic capsule.

The operculum is large as compared with the size of the capsule and is cartilaginous. It has a short columella, but this is not joined to the paraquadrate.

The brain case. — Several dermal bones and the chondrocranium enter into the formation of the brain case. The roof is formed by the frontals and parietals, the floor by the parabasal, while the

cartilaginous rods of the primordial skull and posteriorly the inner borders of the otic capsules form the sides. The foramen magnum is formed by the basi- and supra-occipital arches and the inner walls of the capsules. Between this and the neural arch of the first vertebra, the spinal cord is protected dorsally by thick connective tissue. The frontals are long, thin, transparent bones, contiguous to one another in the mid-dorsal line. On the anterior part of the dorsal surface, each has a slightly roughened area, the articular surface for one of the posterior processes of the premaxillary. Along the outer edge of the ventral surface is a groove which partially invests the dorsal surface of the cartilaginous rod of the primordial skull, and near the posterior border is an articular surface for the parietal, which bone it partially overlaps.

The parietals are somewhat shorter than the frontals, but resemble them closely in structure and relation to each other. On their ventral surfaces are deep grooves, continuous with those on the frontals, investing the rods of the chondrocranium. The postero-lateral angle of the parietal overlaps and articulates with the anterior portion of the otic capsules.

The parabasal is the largest bone of the skull. It is a thin, flat plate, as long as the combined frontal and parietal. The posterior portion is broad and nearly square and the anterior is very long and somewhat narrower, tapering slightly to the anterior border which is bilobed. The ventral surface is smooth, except antero-laterally where it is slightly roughened, articulating with the dorsal surface of the vomers and palato-pterygoids.

Along the lateral borders of the dorsal surface are two articular surfaces on which rest the cartilaginous rods of the chondrocranium which form the sides of the brain case. The posterior ends of these rods lie in small notches at the antero-lateral angles of the broad posterior part of the parabasal. Posterior to these sockets are articular surfaces for the otic capsules and on the middle of the posterior border of the dorsal surface lies the cartilaginous basi-occipital, connecting the otic capsules.

The upper jaw. — The premaxillary, as in Spelerpes, is a single bone, another point in which Typhlomolge differs from the Proteidae. In shape it resembles the Greek letter π. The transverse portion is dentigerous and extends across the snout, being deeply grooved on the posterior surface to encase the broad anterior portion of the

chondrocranium. The two ends of this transverse portion are slightly curved in a posterior direction. The teeth, of which there are from twenty to thirty, are small and pointed, growing out from the ventral surface.

The two posterior processes of the premaxillary are thin splinters of bone arising from the posterior border of the middle third of the transverse portion. Posteriorly they are contiguous, forming a foramen, the fontanelle, between their anterior portions. Their ventral surfaces articulate posteriorly with the dorsal surface of the frontals. The vomers together form a dentigerous arch. These two bones are thin plates with their inner borders contiguous posteriorly and separate anteriorly. The dorsal surface of each is quite smooth, articulating with the parabasal, but the ventral surface has an anterior and lateral ridge on which is a single row of twenty or more teeth.

The palato-pterygoids are irregular narrow plates, each abutting posteriorly on the anterior border of the trabeculo-quadrate isthmus and articulating antero-dorsally with the parabasal and anteriorly with the vomer. Elsewhere they are free from the skull. On its antero-lateral border, each palato-pterygoid bears a row of six or eight teeth, continuous with the row on the vomer.

This skull, on comparison with those of other Urodelous forms, most closely resembles the skull of the Spelerpes larva. The single premaxillary, the bony otic capsules in which the cartilage bones are not differentiated and in which the parachordal region of the chondrocranium is not distinct, the lack of cartilaginous or bony nasal capsules, the arrangement of basi- and supra-occipital arches, and the fact that the operculum is entirely separate from the paraquadrate, are characteristics common to Typhlomolge and the Spelerpes larva, both of which differ in all these points from both Necturus and Proteus.

Vertebral Column.

The vertebral column of Typhlomolge is made up of about fifty [1]

[1] The number and description of vertebrae given here were taken from the larger of my two specimens. In the smaller there were but twenty-eight caudal vertebrae. A comparison of these numbers with the following table taken from Gadow may be of interest: —

	No. trunk vertebrae.	No. caudal vertebrae.
Necturus	19	29
Proteus	30	28
Spelerpes fuscus	16	23

amphicoelous vertebrae. Between the skull and the attachment of the pelvic girdle are fifteen vertebrae, differing but little from one another in shape and size. The sacral vertebra is the sixteenth and the ilia are attached to the ribs which it bears. In the caudal region are thirty-five vertebrae, differing in form from those of the trunk and from one another in size and slightly in form.

The trunk vertebrae. — A typical trunk vertebra consists of a rounded centrum or body to which is attached dorsally the neural

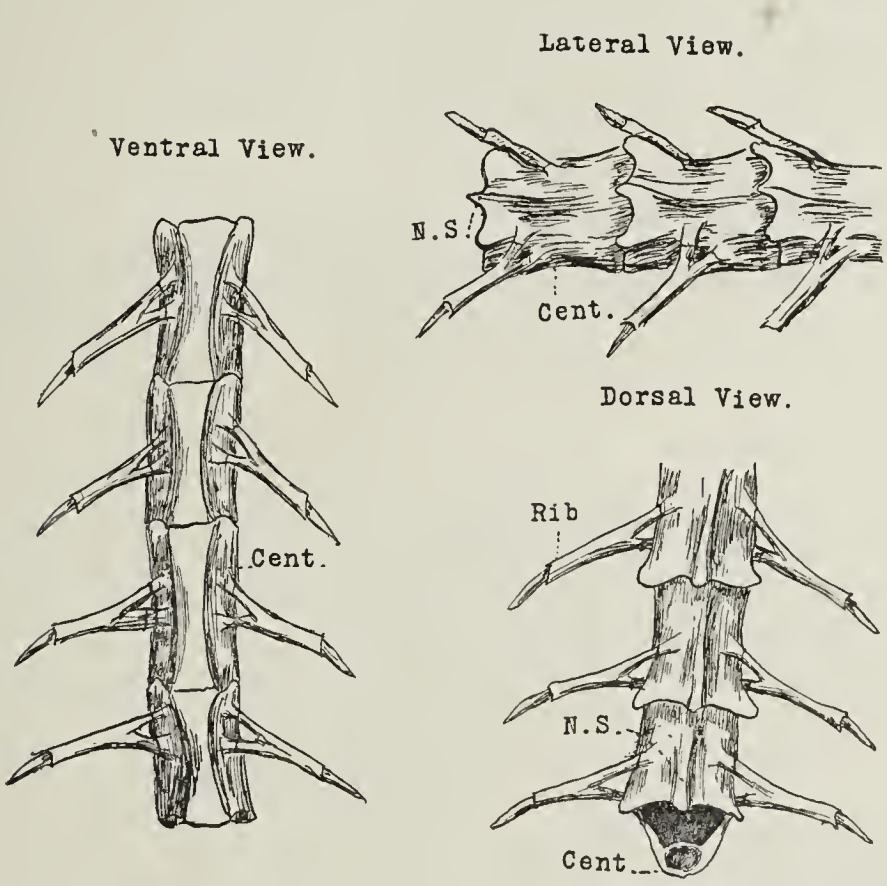

FIG. A.—Trunk vertebrae. × 6. *Cent.*, centrum; *N. S*, neural spine.

arch, bearing a neural spine and two lateral rib-bearing processes. The centrum is in form like an hour-glass with a small concavity at each end, making the vertebra amphicoelous. The rim of the anterior concavity articulates with the rim of the posterior concavity of the vertebra immediately anterior to it.

The dorsal aspect of the neural arch shows a broad plate. In the median line of the posterior half of this plate is a ridge, which becomes very prominent posteriorly, the neural spine. The posterior border of the neural arch slightly overlaps the arch of the vertebra immediately posterior. It bears two postero-lateral processes, the postzygapophyses, the ventral surfaces of which articulate with the

dorsal surfaces of two similar processes, prezygapophyses, borne on the anterior border of the next vertebra posterior. Laterally the neural arch is a thin plate, except at its middle third, from which the heavy transverse process, arising partly from it and partly from the centrum, projects in a postero-lateral direction. The transverse process is made up of two portions, one dorsal and one ventral, each of which articulates distally with the corresponding head of the proximally-forked rib.

The vertebrae are principally bony, the cartilaginous parts being few and hardly distinguishable from the bony ones.

The first vertebra bears no rib and is otherwise modified from the

FIG. B.—Posterior caudal vertebrae, lateral view. × 12. *H. S.*, haemal spine; *N. S.*, neural spine.

typical form. It bears three anterior processes, one median and two lateral, all of which articulate with the skull (odontoid vertebra of W. K. Parker). The median process has a flat, cartilaginous tip, partially encased in bone, which lies dorsal to the basi-occipital arch and is attached to it laterally. Posterior to this, it becomes thicker and broader and is bony, not cartilaginous, finally joining with the two lateral processes to form the body of the first vertebra. The two lateral processes also have cartilaginous tips, encased in bone, which articulate with the occipital condyles.

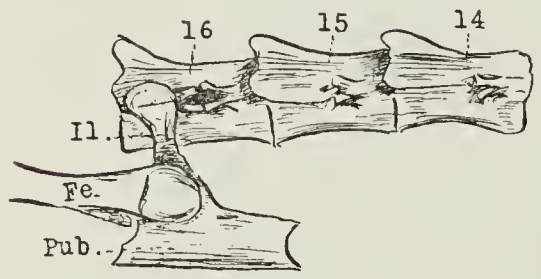

FIG. C.—Attachment of pelvic girdle. × 12. *Fe.*, femur; *Il.*, Ilium; *Pub.*, pubo-ischium.

The body of the first vertebra is anteriorly very broad but narrows rapidly and assumes the hour-glass form. The neural arch is very broad anteriorly, its anterior border being slightly posterior to the joining of the anterior processes to form the body. The transverse process is much less developed than in the other trunk vertebrae.

The sacral vertebra does not differ from the typical form, but the caudal vertebrae are much modified.

The caudal vertebrae. — These are shorter, more compressed, and without transverse processes, so that the lateral plate of the neural arch is increased at the expense of the dorsal one. The transition takes place rapidly in the first three caudal vertebrae, the fourth being typical of the modified form. The neural spine becomes very prominent in the third and continues with little change, disappearing at the 24th or 25th.

The postzygapophyses approach one another and become articular surfaces on the ventral surface of the neural spine. The prezygapophyses also approach each other and are contiguous.

On the fourth caudal vertebra appears the haemal arch, which is typical of the caudal vertebrae in general. It appears suddenly and is formed by two ventral processes from the lateral portions of the centrum uniting distally, thus forming a ventral arch through which the caudal artery passes. This is similar to the neural arch, but somewhat smaller and bears a small rounded haemal spine, projecting postero-ventrally.

This compressed form with a dorsal and a neural arch is found almost unchanged, save for a gradual diminution in size, from the fourth to the 24th or 25th caudal vertebra. Posterior to these, the vertebrae decrease rapidly in size and the neural and haemal spines disappear, the neural arch persisting to the 32d, the haemal arch to the 33d caudal vertebra. The 34th and 35th vertebrae are tiny centra, cylindrical rather than of the hour-glass shape.

The ribs. — The ribs which are borne on the second to the sixteenth vertebra inclusive, differ little in size and form. Each consists of two heads, one dorsal or tubercular and the other ventral or capitular, which articulate with the transverse process of the vertebra and unite to form a shaft. This is slightly longer than the heads and is prolonged distally by a short cartilaginous rod. The rib is flattened antero-posteriorly, the posterior surface being slightly concave. Its general direction is postero-ventral, continuing that of the transverse process. The sacral rib articulates distally with the dorsal end of the ilium, and has no cartilaginous prolongation, but is slightly heavier than the other ribs.

The most important difference in the vertebral column between Typhlomolge and the Proteidae is in the first vertebra. The three long anterior processes by which it articulates with the skull are not found in Necturus or Proteus but they are duplicated in the larval *Spelerpes ruber* (W. K. Parker, '82, pl. 20, figs. 1 and 2).

Visceral Skeleton.

The visceral skeleton consists morphologically of the suspensorium, the mandible, and the hyo-branchial apparatus. The first of these parts has been already considered with the skull.

Mandible.

The mandible consists of two curved cartilaginous rods (Meckel's cartilages), joined anteriorly and diverging posteriorly, giving it an arched shape, and bony plates of dermal origin, three (the dentale, the angulare, and the spleniale) encasing each cartilage.

Meckel's cartilage is anteriorly a cylindrical rod closely joined to the cartilage of the other half of the mandible. Posteriorly it is flattened laterally and widened, its dorso-ventral axis becoming three or four times its original length. The postero-dorsal angle projects slightly and is rounded, articulating with a depression on the distal end of the quadrate.

Of the bony plates, the dentale is the largest, covering the outer surface of the anterior two thirds of the cartilage. Its outer surface is curved inward dorsally and ventrally, so that the inner surface has a marked groove in which the cartilage lies. On the inner surface of the anterior half there is a single row of from twenty to thirty small pointed teeth which project about one half their length beyond its dorsal border. Posterior to this, the dorsal border slopes in a ventral direction forming a very acute angle with the ventral border.

Fitting close to the cartilage, on the posterior half of its inner surface, is the angulare. This bone is a flat splinter, the posterior half being about half the depth of the cartilage, while the anterior portion tapers to a point which reaches nearly to the posterior tooth of the dentale. It bears no teeth.

The spleniale, the third bony plate, is an extremely minute scale bearing dorsally six or eight teeth which are continuous with the row of teeth on the dentale. It lies against the inner dorsal surface of the cartilage, its whole ventral border contiguous with the dorsal border of the angulare at the posterior part of its anterior third. The bony case of the cartilage is therefore not complete, for the posterior third of the cartilage is not covered on its outer surface nor on its inner surface dorsally. The cartilage in this region seems especially thick and tough.

Hyo-branchial Apparatus.

The hyo-branchial apparatus is made up of a series of cartilaginous rods. In the mid-ventral line lie two short cartilages, the first and second basibranchials, the basal elements respectively of the first and second gill arches. The first or anterior basibranchial is short and thick, the second is half as long again and slender, with a slightly enlarged posterior end. From the anterior end of the first basibranchial spring the hyoid cartilages, the longest and thickest of all. These are attached distally by ligaments to the skull, their direction, like that of the mandible and of the branchial arches, being postero-lateral. Posterior to these are the branchial arches, the first of which arises from the posterior end of the first basibranchial and also touches the second basibranchial. It consists of two rods, a short proximal one, the first cerato-branchial, and a longer, slender distal one, the first epibranchial. The second arch, arising from the anterior part of the second basibranchial, is like the first arch but more delicate. The third arch is incomplete, having only an epibranchial cartilage which springs from the posterior border of the second epibranchial at its proximal end. Extending posteriorly from the posterior border of the third epibranchial, at its distal end, is a small raphe, the rudiment of the fourth branchial arch (Göppert, '94; Wilder, '96). No trace of the fifth branchial arch, represented in other forms by the laryngeal cartilage, appears here (*v. infra sub* Respiratory System).

The distal ends of the three epibranchials are contiguous and are attached by the levator muscles to the dorsal region of the head, forming the supports of the three external gill bushes. The gill slits, of which there are three in this animal, open from the pharynx to the exterior, the first between the hyoid and the first epibranchial, the second between the first and second epibranchials, and the third between the second and third epibranchials. The number of gill slits is here different from the number in Proteus and Necturus, for they have but two.

Although as a whole the apparatus is similar to that of the Proteidae, the size and position of the second cerato-branchial and the shape of the second basibranchial make it correspond exactly with the hyoid apparatus of the larval *Spelerpes ruber*.

Appendicular Skeleton.

In Typhlomolge, two of the most striking characteristics are the length of the limbs and the delicate structure of the bones of the limbs and girdles. In these it differs widely from Necturus, Axolotl, and the majority of the Salamandrids, which have short, heavy, thickset bones, and resembles Proteus, though carrying lightness and length of bones to an even greater extreme, a similarity which is correlated with their similar mode of life. The number and arrangement of the carpal and tarsal elements and the number of digits, four on the anterior and five on the posterior limb, are, however, much more suggestive of the Salamandrids than of the Proteidae, and the square shape of the pelvis is much more like that of Spelerpes than like the attenuated form found in Necturus and Proteus.

Pectoral Girdle and Anterior Limb.

In Typhlomolge, the general plan of the pectoral girdle is like that of the other Urodeles. It consists of two lateral plates, largely cartilaginous and quite free from each other and from the axial skeleton, although one overlaps the other slightly in the mid-ventral line. Each plate, which lies close to the trunk muscles, consists of three thin lobes radiating from the glenoid fossa, the dorsal one being the scapula, the antero-ventral the procoracoid, and the postero-ventral the coracoid.

The ventral portion of the scapula, a narrow shaft, widening slightly at each end, is the only bony portion of the girdle, and this is continuous with a broader, dorsal, cartilaginous portion, its dorsal border being opposite the lateral process of the third and fourth vertebrae.

The procoracoid is nearly as long as the scapula, but more slender and very thin, tapering anteriorly to a blunt point.

The coracoid is oval in shape, its posterior border slightly posterior to the shaft of the scapula, and its anterior half lying nearly parallel with the posterior half of the procoracoid. The cartilage about the glenoid fossa is thickened, forming a strong rim about the cavity.

The *humerus* in Typhlomolge is very long and slender. Its

length compared with the distance from the tip of the procoracoid to the anterior border of the glenoid fossa is in the ratio of 10 : 5, while in Proteus the ratio is 8 : 5, and in Necturus 5 : 5.

The humerus, like all the long bones of the limbs, consists of a bony diaphysis and two cartilaginous epiphyses, the proximal one, or head, being rounded and articulating with the glenoid fossa. The diaphysis is flattened both proximally and distally, but in different directions, which gives it a twisted appearance. The proximal third is flattened laterally bearing on its outer surface a ventro-lateral ridge, the crista deltoidea, the insertion of most of the shoulder muscles. The middle third of the diaphysis is more cylindrical in shape, but the distal third is flattened dorso-ventrally, as is the distal epiphysis. The outer portion of this epiphysis is rounded and articulates with a shallow socket on the head of the radius, while the inner portion articulates less firmly with the head of the ulna.

The *ulna* and *radius* are long and thin, their length bearing about the same ratio to that of the humerus as in the Proteidae. The proximal epiphysis of the ulna is slightly prolonged to form the olecranon and is, therefore, somewhat longer than the corresponding epiphysis of the radius. Both bones are flattened dorso-ventrally at their proximal ends. Their distal epiphyses are oblong in shape, that of the radius articulating with the carpal elements, radiale and intermedium, that of the ulna with intermedium and ulnare.

The *carpus* consists of eight small cartilaginous pieces arranged in two rows, three in the proximal and four in the distal one, with the eighth piece, centrale, between. The proximal row contains the largest pieces, the outer being the ulnare, the median the intermedium, and the inner the radiale. The distal row contains carpale 2, 3, 4, and 5, all articulating with centrale, which also articulates with intermedium and radiale. Carpale 1, together with the first digit, is missing. The second, third, fourth, and fifth digits are present, each consisting of a metacarpal, articulating proximally with the corresponding carpale, and one or more phalanges.

There are eight phalanges: one in the second digit, two in the third, three in the fourth, and two in the fifth. The distal ones are very short, each having a cartilaginous proximal epiphysis and a distal bony portion which tapers to a blunt point; the other phalanges and the metacarpals are slightly longer, each having a bony shaft and two cartilaginous epiphyses.

Pelvic Girdle and Posterior Limb.

The pelvic girdle consists of a nearly square ventral plate, the pubo-ischium, corresponding to the pubes and ischia of higher forms, although here these parts are not differentiated. From this spring laterally two slender processes, the ilia, articulating with the distal ends of the sacral ribs and thus attaching the girdle firmly to the axial skeleton. The anterior portion of the pubo-ischium is wholly cartilaginous, having three small anterior projections, one median and the others lateral, but no ypsiloid cartilage is found. I was unable to find obturator foramina. On the middle of the lateral border is the acetabulum which is nearly surrounded by a thickened cartilaginous rim.

The posterior two thirds of the pubo-ischium contain a pair of large centers of ossification, the cartilage persisting as a narrow median strip only. In the mid-ventral region, extending throughout its length, is a ridge for the attachment of muscles, the crista muscularis.

From the outer border of the acetabulum springs the ilium, extending antero-dorsally. The ventral part of the ilium is a flattened, bony shaft, constricted slightly at its dorsal end where it is contiguous with a small cartilaginous epiphysis, with the inner surface of which the sacral rib articulates.

The pubo-ischium is slightly concave on its dorsal surface, thus making more room for some of the viscera.

The *femur* is the longest bone in the body, and, like the humerus, is longer in proportion to the size of the animal than the femora of allied forms. It is much like the humerus in shape, having a rounded cartilaginous proximal epiphysis which articulates with the acetabulum, a long, cylindrical, bony shaft less flattened proximally than that of the humerus, and a slightly rounded distal epiphysis which articulates internally with the proximal end of the fibula and externally with the proximal end of the tibia.

There is a ventral ridge or trochanter on the proximal end of the femur and on the outer surface is a small lateral ridge, both being used for the attachment of muscles. The trochanter seems to correspond in position to the lesser trochanter of higher forms, but may not be morphologically the same.

The *tibia* and *fibula* correspond closely in shape and position to the ulna and radius, respectively. The tibia is, however, perceptibly larger than the fibula and articulates more completely with the femur.

The *tarsus* consists of eight pieces arranged like those of the carpus in two rows around a central piece. The fibula articulates with the fibulare and the intermedium; the tibia with the intermedium and the tibiale. The centrale articulates with all the other tarsal elements. Tarsale 4 and 5 are here represented by one piece articulating with the metatarsals of the fourth and fifth digits. Tarsale 1, 2, and 3 are separate, each articulating with the metatarsal of the corresponding digit.

The phalanges are twelve in number: one in the first digit, two in the second, three in the third, three in the fourth, and two in the fifth. Together with the metatarsals, they are similar in shape and structure to the corresponding parts of the manus.

The number and arrangement of both tarsal and carpal elements, with the exception of the fusion of tarsale 4 and 5, are identical with those of the *Spelerpes ruber* larva

Muscular System.

The muscles are in number and arrangement much like those of Proteus and Necturus. On the dorsal, lateral, and ventral surfaces of the trunk and tail are simple undifferentiated muscle masses, metameric in structure, like muscles of those regions in the fish. The more specialized muscles are those of the head, moving the jaws and the hyoid apparatus, and of the pectoral and pelvic regions, allowing for free movement of the limbs. This arrangement is parallel to that found in most aquatic animals to which the movement of the limbs in swimming and walking, and of the jaws in feeding, is much more important than movement of the body proper, except in simple contortions.

In Typhlomolge, however, the muscles of the limbs are more delicate than those of Necturus. According to Norman, when in rapid motion the animal uses its tail as well as its legs, the ordinary movements of the animal being very slow. This may explain the lack of development in the limb muscles.

Histologically, too, all the muscles of Typhlomolge differ markedly

from those of Necturus and Proteus in that the bundles of fibers are more widely separated from one another. This is also apparent in dissection.

In treating more particularly of the muscles, they may be classified for convenience as follows:—

1. Muscles of the Head	a. of the mandible.	
	b. of the hyoid apparatus.	
2. Muscles of the Trunk	a. of the trunk proper.	
	b. of the tail.	
3. Muscles of the Fore Limb	a. of the dorsal surface	extrinsic.
		intrinsic.
	b. of the ventral surface	extrinsic.
		intrinsic.
4. Muscles of the Hind Limb	a. of the ventral surface	outer layer.
		deep layer.
	b. of the dorsal surface	outer layer.
		deep layer.

Owing to lack of time, the muscles of the gill bushes, of the fore limb distal to the humerus, and of the hind limb distal to the femur have not been worked out. In some cases I could not find the origin nor the insertion of a muscle owing to the fact that one specimen was already partly dissected when I received it and that the anterior part of the other was kept intact for sectioning.

Muscles of the Head.

Muscles of the Mandible.

The muscles used in moving the lower jaw are well developed, and form the thick mass covering the top of the skull and the ventral surface of the head.

The *temporalis* (fronto-parieto-maxillaris) arises from the mid-dorsal region of the frontal and parietal (anterior part) as a thick, well developed muscle, and tapers to a tendinous insertion on the middle third of the dorso-lateral surface of the mandible below the eye.

The *masseter* (petro-tympano-maxillaris) a thick, oblong muscle, arises from the outer part of the parietal and lies parallel with the posterior border of the temporalis, partially covering it at its distal

end, inserting posterior to it on the mandible. The action of these two muscles is to close the jaws.

The *digastric* (cephalo-dorso-maxillaris) is a large thick muscle arising by two heads, one from the parietal, postero-lateral to the masseter, the other from the anterior border of the distal end of the first epibranchial, posterior to the cerato-hyoideus externus. Both heads uniting, insert on the mandible posterior to its articulation. The action of this muscle is to open the jaws.

The *mylo-hyoideus* (intermaxillaris anterior) is a thin delicate sheet arising from the inner ventral surface of the anterior half of the mandible and inserting with its fellow in the mid-ventral line.

The *stylo-hyoideus* (intermaxillaris posterior) consists of two parts. The anterior, a delicate fan-shaped sheet, arises from the anterior border of the distal end of the hyoid and inserts with its fellow in the mid-ventral line, covered by the mylo-hyoid. The posterior part is a somewhat thicker sheet arising from the posterior border of the distal part of the first epibranchial, median to the insertion of the cerato-hyoideus externus, and inserting like the anterior part and posterior to it. These two intermaxillary muscles serve to hold the hyoid apparatus more firmly in place and by their contraction and expansion it can be raised and lowered slightly to allow for the fluctuation of the throat in breathing.

The *genio-hyoideus* is a very long and slender, paired muscle arising from the inner surface of the mandible near the symphysis, covered by the intermaxillaries, and inserting on the posterior end of the second basibranchial. As seen from the ventral aspect, it forms a conspicuous double band lying in the median line.

Muscles of the Hyoid Apparatus.

The muscles of the hyoid apparatus are much like those of Necturus and Proteus, the most important difference being the presence of a levator arcus primi which is attached to the first epibranchial. The ventral aspect shows the following muscles: —

The *cerato-hyoideus externus* is the largest of the hyoid muscles. It arises from the antero-proximal border of the ventral surface of the hyoid and is inserted on the anterior border of the distal end of the first epibranchial, median to the origin of the second head of the digastric.

The *cerato-hyoideus internus*, a smaller and more slender muscle, arises from the postero-ventral border of the proximal end of the hyoid and, widening, inserts on the postero-ventral surface of the proximal end of the first epibranchial.

The *thoracico-hyoideus* consists of two long and rather thick muscles, the *sterno-hyoideus* and the *omo-hyoideus*. I was unable to find their origin, but from analogy with Proteus and Necturus, I should expect it to be with the origin of the rectus abdominis on the posterior border of the first cerato-branchial. Both muscles lie ventral to the rectus abdominis and are almost contiguous to it anteriorly. Posteriorly they diverge from it and from each other, inserting separately, the sterno-hyoideus on the inner surface of the shoulder girdle between the procoracoid and the coracoid, the omo-hyoideus with the trapezius on the inner surface of the girdle between the procoracoid and the scapula.

The *two interbranchiales* (the subcerato-branchiales of Drüner), are slender, very short muscles, parallel to each other. The first has two heads, (a) and (b); (a) arises from the proximal end of the first epibranchial at its antero-ventral border, distal to the cerato-hyoideus internus, thus traversing the entire width of the cartilage, and passes dorsal to the adductor arcus tertii; (b) has a similar origin, distal to (a), and passes ventral to adductor arcus tertii, inserting with (a) on the postero-ventral surface at the proximal end of the third epibranchial. The second interbranchial takes its origin from the antero-ventral surface at the proximal end of the second epibranchial and inserts near the first interbranchial, distal to portion (b).

The *two adductores arcuum* are short, slender muscles associated with the second and third gill arches; that of the second gill arch arises from the first myocomma of the rectus abdominis and inserts on the ventral surface of the second epibranchial at its proximal end; that of the third gill arch arises from the second myocomma of the rectus abdominis and inserts on the ventral surface of the third epibranchial at its proximal end.

The remaining hyoid muscles are best seen from a dorsal aspect.

The *levatores arcuum* serve to raise the gill arches, and are five in number. The *first* is short and thick, arising from the temporal region of the skull posterior to the first head of the digastric. It is covered distally by the cerato-hyoideus externus and inserts at the

distal end of the first epibranchial on its pharyngeal surface. The *second* and *third* are short and thinner than the first. They arise from the first myocomma of the back muscle, posterior to the temporalis, and pass backwards and outwards to insert respectively on the second and third epibranchials, on the pharyngeal surface at their distal ends. The *fourth* is much thicker than either the second or the third and arises from the integument of the back by fascia, inserting on the outer side of the lateral raphe which extends posteriorly from the distal end of the third epibranchial, according to Göppert ('94) and Wilder ('96) the supposed rudiment of the fourth epibranchial. The *fifth* is in form and origin similar to the fourth and probably inserts on the mid-ventral line with its fellow, although I was unable to verify this, owing to the fact that the specimen had been partially dissected before I received it. It is evident that this fifth levator arcus is identical with the dilatator laryngeus of allied forms, thus emphasizing the serial homology of this last-named muscle with the other levators. Here they evidently belong to the same series and are so treated.

The *hyo-trachialis* (the interbranchialis of Drüner) is a thin sheet of muscle forming the floor of the pharynx. It is divided into two parts, the anterior arising from the posterior border of the middle third of the third epibranchial, and the posterior from the inner edge of the raphe which represents the fourth epibranchial. Both parts insert with their fellows in the mid-ventral line, owing to the absence of a trachea.

Muscles of the Trunk.

The trunk muscles of Typhlomolge are large thick masses, metameric in structure and little differentiated (the thoracico-hyoideus, described above, is possibly a differentiation of the rectus abdominis).

Along the back runs a very thick, paired muscle, the two portions being parallel and separated only by a narrow band of connective tissue containing fat. It arises from the postero-dorsal part of the skull and extends to the sacral region where it is continued in a ventral direction and is continuous with the lateral muscle of the tail. The fibers run from myocomma to myocomma, a few of the inner ones attaching to each vertebra.

Laterally the trunk is covered from the shoulder to the pelvis by

three muscular sheets: the external and the internal oblique, and the transversalis, all having their origin ventral to the back muscle on the outer border of the ribs. I was unable to demonstrate their insertion with certainty, but it was apparently on the edge of the rectus abdominis by aponeurosis. It is probable that this aponeurosis envelops the rectus, conforming to the usual arrangement in allied forms. The fibers of the external oblique run from their origin postero-ventrally, those of the internal oblique run from their origin antero-ventrally, and those of the transversalis, which is interior to the internal oblique, run nearly dorso-ventrally, slanting a little to the anterior. All these muscles are divided into segments by myocommata.

The *rectus abdominis* (pubo-hyoideus) is a paired muscle similar to the back muscle. It arises from the postero-ventral border of the first cerato-branchial and inserts on the antero-ventral surface of the pubo-ischium in the mid-ventral region, separated from its fellow by the linea alba, and covered in the region of the shoulder girdle by the coracoids and the pectoralis.

In the caudal region the vertebrae are flattened and the dorsal muscle becomes compressed and extended ventrally so that it forms a thin lateral sheet, that meets its fellow in both the mid-dorsal and mid-ventral lines. Some of its fibers are attached to the lateral surface of each vertebra.

Muscles of the Fore Limb.

Dorsal Surface.

In describing the dorsal muscles of the fore limb, I shall divide them into two groups, the extrinsic (those that are attached by one end to the girdle or limb) and the intrinsic (those that are attached at both ends to the girdle or limb).

Extrinsic muscles.— The *levator scapulae* is a short thick muscle, whose origin I was unable to ascertain, although it is probably the postero-dorsal border of the skull as in Proteus. It inserts on the antero-dorsal border of the inner surface of the scapula and serves, with the trapezius, to draw the scapula upward and forward.

The *trapezius* (cucullaris), a thick fan-shaped sheet, arises with its fellow from a mid-dorsal aponeurosis, anterior to the scapula, and

inserts on the anterior border of the scapula, dorsal to the omo-hyoideus.

The *latissimus dorsi* is similar to the trapezius in shape and origin, but it arises posterior to the scapula. It inserts on the dorsal part of the posterior border of the scapula. It serves, with the serratus magnus, to draw the scapula upward and backward.

The *serratus magnus* (thoracico-scapularis), a short thick muscle, arises by two heads, one from the inner surface of the scapula near the postero-dorsal angle and the other anterior to this. Both parts unite and probably insert on the third or fourth rib, though I was unable to determine this with certainty.

Intrinsic muscles. — On the outer surface of the scapula lies the *supra-scapularis*, arising from the dorsal portion of the outer surface, with the exception of the anterior and the dorsal border, and inserting on the dorsal part of the head of the humerus.

On the inner surface of the scapula, arising from the antero-ventral part of it and the posterior part of the procoracoid, is a slender V-shaped muscle, *subscapularis*, inserting on the inner dorsal part of the proximal end of the humerus, between anconeus coracoideus and anconeus scapularis medius.

Ventral Surface.

The muscles of the ventral surface are also divided into two groups, extrinsic and intrinsic.

Extrinsic muscles. — The *pectoralis*, by far the largest muscle of the fore limb, is a superficial sheet partially covering the supracoracoideus and the rectus abdominis. Its anterior portion arises with the corresponding part of its fellow from the mid-ventral line, its posterior portion from the rectus abdominis and the aponeurosis of the external oblique. Its fibers converge to its insertion on the distal part of the lateral process of the humerus. It acts as an adductor of the fore limb.

Intrinsic muscles. — The *coraco-brachialis longus*, a slender spindle-shaped muscle, arises from the posterior border of the procoracoid near the anterior rim of the glenoid fossa and inserts on the distal two thirds of the inner surface of the humerus.

The *coraco-brachialis brevis* is much shorter and very slender. It arises from the postero-ventral border of the coracoid, and is cov-

ered by the supra-coracoideus ; it inserts on the head of the humerus between the coraco-brachialis longus and the coraco-radialis proprius.

The *supra-coracoideus*, very similar to the supra-scapularis, is a fan-shaped sheet arising from the ventral part of the outer surface of the coracoid, except the ventral and anterior borders. Its insertion on the head of the humerus is covered by the pectoralis.

The *coraco-radialis proprius*, seeming almost like a thin and tendinous continuation of the procoraco-humeralis, takes its origin from the posterior edge of the coracoid on a line continuous with the main axis of the procoracoid. It inserts on the head of the radius with the humero-antibrachialis inferior.

The *procoraco-humeralis* is a thin narrow band covering the procoracoid, and arising from the anterior border of its outer surface. It inserts dorsally to the supra-coracoideus on the head of the humerus.

The *humero-antibrachialis inferior*, a slender spindle-shaped muscle, acting with coraco-radialis proprius as the flexor of the fore limb, arises from the ventral side of the lateral process of the humerus and inserts on the inner surface of the head of the radius.

The *anconeus* is the chief extensor of the fore limb and has several parts, all long and slender muscles, arising separately and uniting to insert on the olecranon. Their origins are as follows : —

Anconeus coracoideus from the posterior border of the coracoid near the glenoid fossa.

Anconeus scapularis medius from the postero-ventral edge of the scapula.

Anconeus humeralis lateralis from the lateral process of the humerus, dorsal to the humero-antibrachialis inferior.

I was unable to find anconeus humeralis medius in Typhlomolge and it also seemed to be absent in Proteus. In both animals the limb muscles are delicate, as there is little weight to be supported, and probably this fourth head has disappeared or is included in the anconeus humeralis lateralis.

Muscles of the Hind Limb.

Ventral Surface.

Outer layer. — The *semitendinosus* (pubo-ischio-tibialis) is a thick, broad, superficial sheet arising from the posterior half of the

crista muscularis of the pubo-ischium. It tapers rapidly, the distal two thirds being very slender, and inserts on the outer surface of the proximal end of the tibia.

The *semimembranosus* (ischio-flexor), a long slender muscle arising from the postero-lateral angle of the pubo-ischium, is covered by the semitendinosus at its origin and inserts ventral to it on the proximal end of the tibia.

The *pubo-tibialis*, a very slender spindle-shaped muscle, arises from the antero-lateral angle of the pubo-ischium and inserts dorsal to the semitendinosus.

These three muscles serve as flexors of the hind limb.

The *ischio-caudalis* is a thick and rather broad muscle arising from the posterior border of the pubo-ischium and uniting with the lateral caudal muscle mass at the second myocomma posterior to the cloacal orifice.

The *caudali-pubo-ischio-tibialis*, a long and very slender muscle, arises with piriformis (caudali-femoralis) from the fifth or sixth caudal vertebra and is covered posterior to the cloacal orifice by the ischio-caudalis. Its fibers join those of the semitendinosus on the inner surface of that muscle, near the postero-lateral angle of the pubo-ischium.

These two muscles are flexors of the tail, hence the attachment of caudali-pubo-ischio-tibialis to the caudal vertebrae, described above as its origin, is physiologically its insertion.

Deep layer.— The *pectineus* (pubo-ischio-femoralis externus), a broad thick sheet, arises from the whole length of the crista muscularis of the pubo-ischium, covered posteriorly by semitendinosus, and tapers rapidly to its insertion on the outer surface of the trochanter of the femur. Anteriorly it covers the insertion of the rectus abdominis.

The *adductor* (pubo-ischio-femoralis internus), a thin, delicate, narrow sheet, arises from the antero-lateral portion of the dorsal surface of the pubo-ischium. Emerging, it passes over the head of the femur and inserts on the proximal fourth of its outer surface, dorsal to pectineus.

The *quadratus femoris* (ischio-femoralis) is a very short and thick muscle covered by pectineus, arising from the postero-lateral angle of the pubo-ischium and inserting on the ventral part of the trochanter of the femur.

These three muscles are the adductors of the posterior limb.

The *piriformis* (caudali-femoralis), a thin, slender muscle covered posteriorly by ischio-caudalis, arises from the fifth or sixth caudal vertebra with caudali-pubo-ischio-tibialis and inserts on the trochanter of the femur distal to ischio-femoralis. It acts singly as an abductor, and with its fellow as a flexor of the tail.

Dorsal Surface.

Outer layer.— The *ilio-extensor*, a narrow sheet, arises from the outer surface of the ilium and inserts on the inner dorsal surfaces of the head of the fibula.

The *ilio-fibularis* may be possibly a part of the ilio-extensor, for its origin and insertion are contiguous to those of ilio-extensor and immediately ventral to them. In Necturus a second head is found in this muscle and it is thus a biceps femoris, but in Proteus and Typhlomolge but one head appears.

The ilio-extensor and ilio-fibularis are the extensors of the hind limb.

Deep layer.— The *ilio-femoralis* is a delicate tapering sheet, taking its origin from the outer surface of the ilium, covered by the ilio-fibularis, and inserting distal to the adductor on the ventral surface of the femur. It acts as an abductor of the hind limb.

Urogenital System.

The urogenital system does not show any marked difference from the general Urodelous type.

Both my specimens were females, one only being mature, so that no account of the male reproductive organs can be given.

The kidneys, lying close together against the dorsal muscle, are very thin and delicate. They extend from the shoulder nearly to the cloacal orifice, the anterior half being very narrow and thread-like, while the posterior half is much broader. The ureters lie along the outer borders of the kidneys and open into the posterior portion of the dorsal wall of the cloaca. A urinary bladder is present, opening into the cloaca near the middle of its ventral wall. The bladder is long and thin, and lies ventral to the intestine. It is connected anteriorly by a membrane with the posterior end of the liver.

The ovaries are ventral to the posterior half of the kidneys and dorsal and lateral to the intestine. In the mature specimen each contained fifteen or twenty large yellow eggs, nearly spherical in shape and about 1.5 mm. in diameter. In the other specimen the ovary was small and immature, whitish in color and slightly granu-

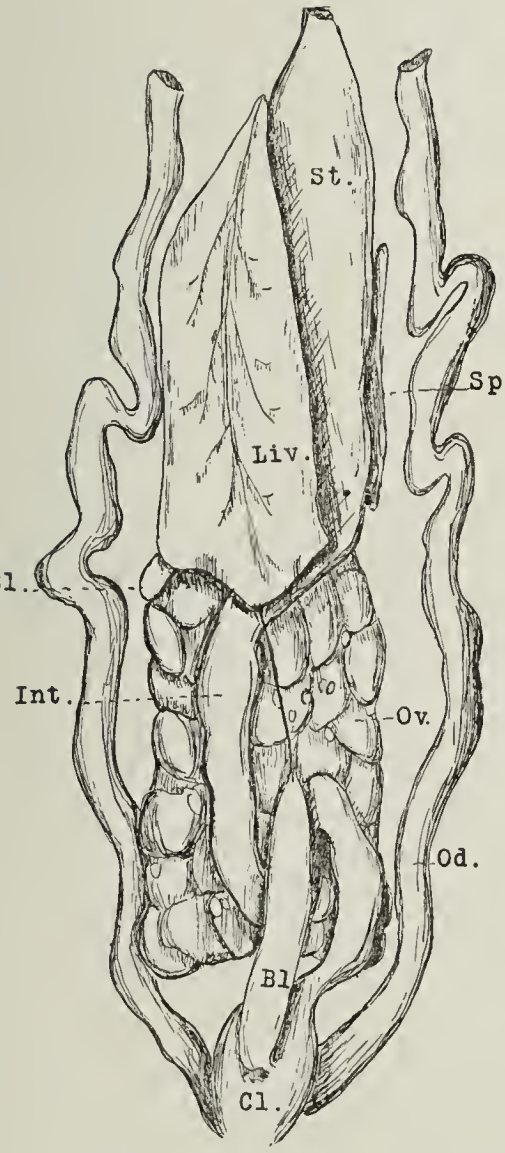

FIG. D.—Viscera, ventral view. × 3. *Bl.*, bladder; *Cl.*, cloaca; *G. Bl.*, gall bladder; *Int.*, intestine; *Liv.*, liver; *Od.*, oviduct; *Ov.*, ovary; *Sp.*, spleen; *St.*, stomach.

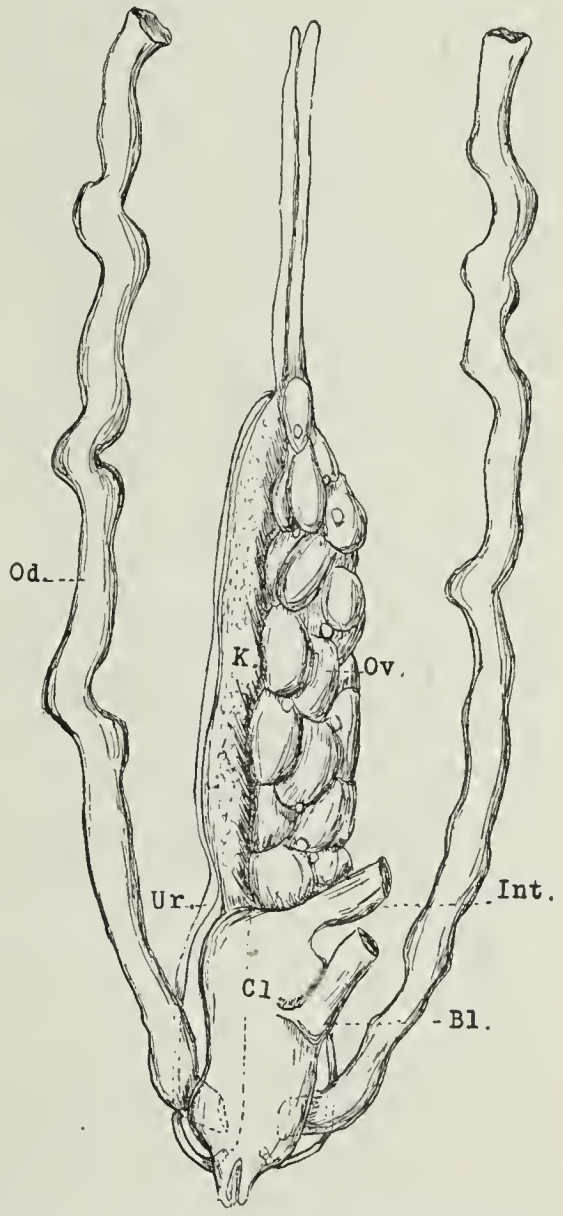

FIG. E.—Urogenital system, ventral view. × 3. *Bl.*, bladder; *Cl.*, cloaca; *Int.*, intestine; *K.*, kidney; *Od.*, oviduct; *Ov.*, ovary; *Ur.*, ureter.

lar in appearance. Here the oviducts were not developed, but in the mature specimen they were large, white, convoluted tubes extending from under the coracoids to the cloaca in a dorso-lateral position. They open into the cloaca dorso-laterally, anterior to the openings of the ureters. They did not contain eggs.

Digestive System.

The digestive system of Typhlomolge corresponds very closely to those of the other Urodeles.

The mouth is provided with three sets of teeth: the premaxillary row, the vomero-palatine row, and the mandibular row; it contains the tongue which is free at the anterior border. It opens posteriorly into the wide pharynx, which in turn narrows into a thin-walled esophagus. The esophagus is long, extending posteriorly to the middle of the coracoids where it widens into the stomach. Its inner surface is much folded.

The stomach is large and cylindrical with thicker muscular walls, and extends half way to the cloaca. Its width is about one fifth of its length. It is partially covered ventrally throughout its length by the liver, a large, well developed, whitish organ, apparently free from pigment.

Connected with the posterior portion of the liver is a small gall-bladder from which the hepatic duct passes to the intestine, near its junction with the stomach. On the dorsal wall of the stomach lies a small three-lobed pancreas with a duct that opens into the intestine near the hepatic duct. The stomach contained a partially digested mass in which were found the head and thorax of an unknown grasshopper, with very large eyes, and a worm, closely resembling an Acanthocephalus, although no hooks were visible.

The posterior part of the alimentary canal is a large, slightly coiled intestine, nearly twice as long as the stomach. This opens posteriorly into the large rounded cloacal chamber, which lies on the dorsal surface of the pubo-ischium. The urogenital system also opens into this chamber. Its external orifice is a longitudinal slit immediately posterior to the pelvic girdle in the mid-ventral line. This is nearly surrounded by a glandular mass, lying between the two ischio-caudal muscles.

Ductless Glands.

Sections of the head reveal the presence of a thymus gland, but I do not find thyroids. The thymus here, as in the Spelerpes larva, is subcutaneous and dorsal to the gill bushes.

The spleen lies slightly dorsal to the middle third of the stomach.

Nervous System.

Owing to lack of material, the nervous system has not been studied. Being the most conservative system, it probably would differ so slightly from that of Urodeles in general, that to find wherein it differed would necessitate a special study, more detailed than the scope of this paper would permit. A few words, however, may be said of the sense organs.

The nasal cavity has no cartilaginous or bony capsule, and in my specimen, owing to the method of preservation, its epithelial lining has disappeared except for an occasional very small space. The anterior nares are at the antero-lateral angles of the snout and the posterior ones are nearer to the median line and slightly anterior to the ante-orbital processes. The nasal cavity therefore makes an acute angle with the longitudinal axis of the head.

The eye is functionless, being devoid of lens, rods and cones, and muscles (Eigenmann, :00).

The otic capsule contains the three semicircular canals, the imprint of which is so strong as to be clearly visible on the outer surface of the capsule. On the ventral surface the imprints of the anterior and longitudinal canals appear, and on the dorsal surface the imprint of the posterior canal.

Circulatory System.

Fresh specimens would be necessary for the study of the circulatory system. In the preserved specimens, the heart appeared to have but one atrium. According to Bruner (:00), this is usual with lungless salamanders, and is due probably to the confluence of the original two.

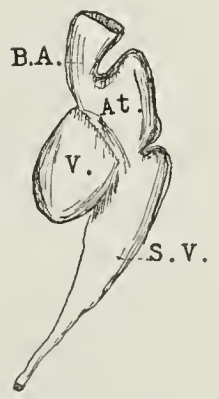

Fig. F. — Heart, left side. × 6. *At.*, atrium; *B. A.*, bulbus-arteriosus; *S. V.*, sinus venosus; *V.*, ventricle.

Respiratory System.

There is no pulmonary system in Typhlomolge, for dissection shows no lungs, trachea, larynx, nor laryngeal cartilages, nor is any trace of them found in the serial cross sections. The respiratory

system is therefore quite different from that of the Proteidae and is exactly like that of the larvae of the lungless Salamandrids, as the animal breathes by its external gills and probably to some extent by its skin. There are three external gill bushes on each side of the head, attached to the branchial arches, and three gill slits on each side, allowing the free passage of water through the pharynx. This arrangement of gill bushes and gill slits is closely similar to that found in the larval Spelerpes, but in the Proteidae the two posterior only of these gill slits appear. It is possible that the walls of the pharynx and esophagus may be also concerned in respiration, as is the case in the adult forms of Desmognathus and of Spelerpes as described by Miss Barrows (:00) and Wilder ('96).

Summary and Conclusion.

Aside from its extraordinary proportions, which may be the result of its strange habitat and mode of life, as Stejneger suggests, it is evident from the preceding description of the various systems and their comparison with those of allied forms, that Typhlomolge in most of its structural peculiarities shows a marked resemblance to the Spelerpes larva.[1] It is equally true that these similarities are the very points in which it differs widely from the Proteidae. In color, in the possession of non-functional, subcutaneous eyes, and in slenderness of limb, Typhlomolge does resemble Proteus, but these common characteristics may be due to their similar surroundings and manner of life, and seem hardly fundamental enough to warrant the placing of both forms in the same family, especially when the very large number of important structural similarities to Spelerpes is considered. The following tabular summary may help to make these points clear.

Spelerpes Larva and Typhlomolge.	Necturus and Proteus.
Number of gill slits, 3.	Number of gill slits, 2.
Number of fingers, 4.	Number of fingers, 4 (N) ; 3 (P).
Number of toes, 5.	Number of toes, 4 (N) ; 2 (P).

[1] I have compared it carefully with the *Spelerpes ruber* larva, and found the resemblance especially strong in that form. Specimens of the other species were not at hand, but from plates of Parker ('82), Wiedersheim ('75), and others, the similarities are plainly apparent, though somewhat less marked.

Second basibranchial slender, and slightly enlarged posteriorly.	Second basibranchial broader, less enlarged posteriorly.
Second cerato-branchial springs from the anterior part of second basibranchial.	Second cerato-branchial springs from the distal end of first cerato-branchial.
Nasal capsules membranous.	Nasal capsules cartilaginous.
Operculum free from paraquadrate.	Operculum attached to paraquadrate.
Otic capsule entirely bony; configuration of semicircular canals visible externally; exoccipital, opisthotic, and pro-otic elements not distinguishable.	Otic capsule partly cartilaginous; configuration of semicircular canals not visible externally; exoccipital, opisthotic, and pro-otic elements forming separate centers of ossification and therefore distinguishable.
Supra-occipital arch connects middle third of otic capsules.	Supra-occipital arch connects cartilaginous part of capsules (N); opisthotics (P).
First vertebra with three long anterior processes articulating with the skull, the median one contiguous ventro-laterally to the basi-occipital arch.	First vertebra without such processes.
Number of carpal pieces, 8; arrangement identical.	Number of carpal pieces, 6 (N); 3 (P).
Number of tarsal pieces, 8 (T); 9 (S). (In Typhlomolge, tarsale 4 and 5 are fused, otherwise arrangement is identical.)	Number of tarsal pieces, 6 (N); 3 (P).
Length of pelvis equal to breadth; 3 very small anterior processes (1 median and 2 lateral).	Length of pelvis much greater than breadth; 1 large median anterior process (N); 3 large anterior processes (P), (1 median and 2 lateral).
No lungs, trachea, nor larynx, even in rudimentary state.	Lungs, trachea, and larynx present.

In view of these various similarities to Spelerpes and differences from the Proteidae, I am strongly of the opinion that Typhlomolge should be classed with Spelerpes in the family Salamandridae and the subfamily Plethodontinae.

The persistence of the gills and the retention of other larval characteristics, after the animal is sexually mature, is a phenomenon of rather frequent occurrence among the Urodeles (such cases have been reported in *Triton vulgaris*, *Triton alpestris*, *Triton cristatus*, *Triton boscai*, *Triton waltli*, and Amblystoma). According to Gadow, it is looked upon by some authorities as "the result of

adaptation to the surroundings, which make it advantageous for the creature to retain its larval features," while "others think that the surroundings somehow or other retard or prevent the assumption of the adult characters." It may be possible, therefore, that Typhlomolge is a form closely akin to Spelerpes, whose retention of larval characteristics, although sexually mature, is a result of its environment and that in other surroundings it might, as was the case with Axolotl, undergo metamorphosis.

Note. — Since this paper left our hands, an article has appeared on the Rank of Necturus among tailed Batrachia (Biol. bull., vol. 8, 1905, p. 67–74) in which the author, Dr. B. F. Kingsbury, takes the ground that Necturus and Proteus are permanent larvae and suggests, although with no investigation, that Typhlomolge will be found to be in the same condition. We hope that Dr. Kingsbury will continue his studies in this direction and ascertain, if possible, the adult forms with which Necturus and Proteus are related. Their place can hardly be among the Plethodontidae, as this author suggests, since all the members of this family are, so far as is known, lungless, a condition which allows Typhlomolge to be included within this family, but seems to exclude the others.— H. H. Wilder.

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'96a. The amphibian larynx. Zool. jahrb., abth. f. anat. u. ontog., vol. 9, p. 273–318, pl. 19–21.

:03. The skeletal system of *Necturus maculatus* Rafinesque. Mem. Boston soc. nat. hist., vol. 5, p. 387–439, pl. 62–67, text-fig. 1–22.

Printed February, 1905.

EXPLANATION OF PLATES.

The outlines of the figures were drawn with a camera. The numbers giving the enlargement are approximate. The figures for the plates were originally drawn in color by the author and have been redrawn in black and white by Dr. H. H. Wilder for the present publication.

Abbreviations Used.

Bones.

ANG. Angulare.
DENT. Dentale.
F. Frontal.
FB. Fibula.
FM. Femur.
H. Humerus.
IL. Ilium.
MC. Metacarpals.
MT. Metatarsals.
O. Operculum.
P. Parietal.
PB. Parabasal.
PE. Periotic.
PH. Phalanges.
PMX. Premaxillary.
PQ. Paraquadrate.
Q. Quadrate.
R. Radius.
SC. Scapula.
SPL. Spleniale.
T. Tibia.
UL. Ulna
V. Vomer.

Muscles.

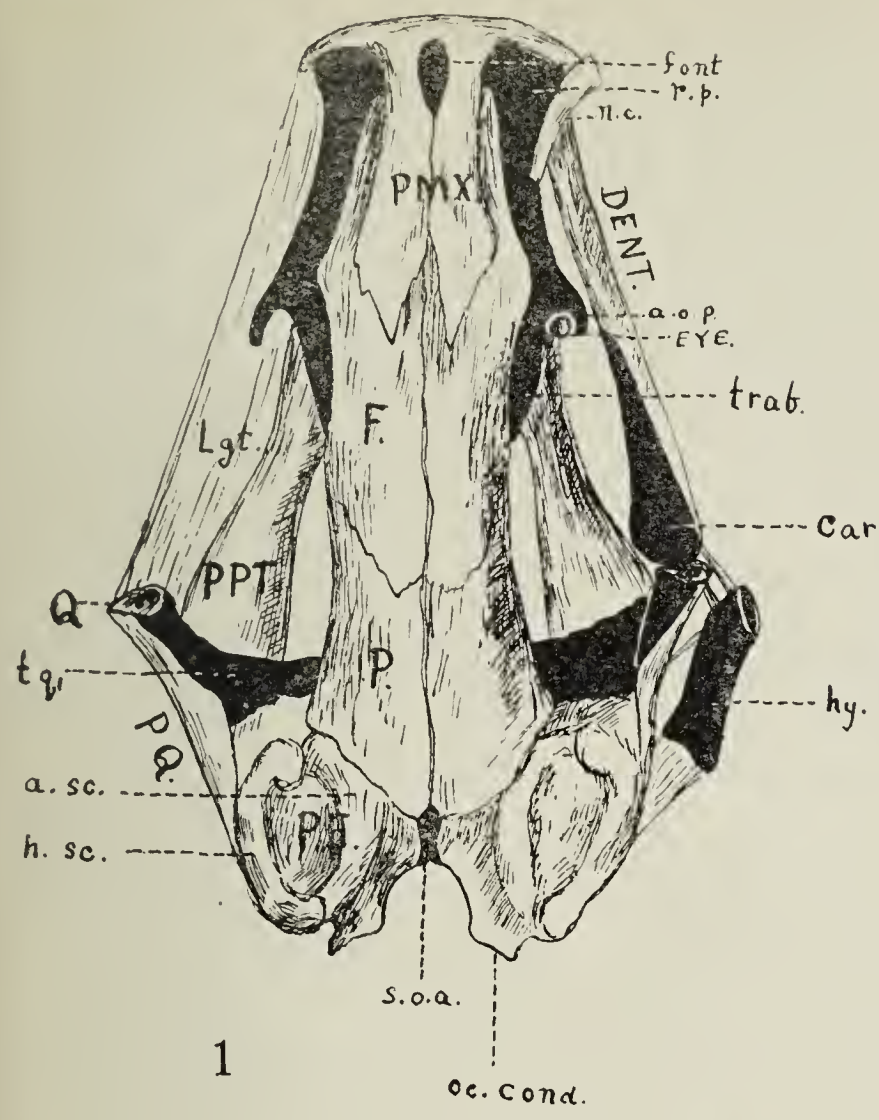
aa., 2–3. Adductores arcuum.
ac. Anconeus coracoideus.
ahl. Anconeus humeralis lateralis.
asm. Anconeus scapularis medius.
cbb. Coraco-brachialis brevis.
cbl. Coraco-brachialis longus.
cf. Piriformis.
che. Cerato-hyoideus externus.
chi. Cerato-hyoideus internus.
cpit. Caudali-pubo-ischio-tibialis.
crp. Coraco-radialis proprius.
dg., 1–2. Digastric.
exo. External oblique.
fpm. Temporalis.
gh. Genio-hyoideus.
hai. Humero-antebrachialis inferior.
ht., 1–2. Hyo-trachiales.
ib., 1–2. Interbranchiales.
ic. Ischio-caudalis.
ifl. Semimembranosus.
ilext. Ileo-extensor.
ilf. Ileo-femoralis.
ilfi. Ileo-fibularis.
ima. Mylo-hyoideus.
imp. Stylo-hyoideus.
isf. Quadratus femoris.
la., 1–5. Levatores arcuum.
ld. Latissimus dorsi.
ls. Levator scapuli.
omh. Omo-hyoideus.
pect. Pectoralis.
ph. Procoraco-humeralis.
pife. Pectineus.
pifi. Adductor.
pit. Semitendinosus.
pt. Pubo-tibialis.
ptm. Masseter.
ra. Rectus abdominis.
sc. Supra-coracoideus.
sm. Serratus magnus.
ss. Supra-scapularis.
sth. Sterno-hyoideus.
sub. sc. Subscapularis.
trap. Trapezius.

Other Designations.

a-o. p. Ante-orbital process.
a. sc. Anterior semicircular canal.
bb., 1–2. Basibranchials 1–2.
b-o. a. Basi-occipital arch.
c., 1–5. Carpals 1–5.
cart. Mk. Meckel's cartilage.
cb., 1–2. Cerato-branchials 1–2.
col. Columella.
cor. Coracoid.
cr. delt. Crista deltoidea.
cr. lat. Crista lateralis.
cr. musc. Crista muscularis.
cr. vent. Crista ventralis.
eb., 1–3. Epibranchials 1–3.
fib. Fibulare.
f. o. Foramen ovale.
font. Fontanelle.
foss. acet. Fossa acetabularis.
h. sc. Horizontal semicircular canal.
hy. Hyoid.
in. Intermedium.
lgt. Ligament.
lgt. h-s. Ligamentum hyo-suspensoriale.
lgt. m-h. e. Ligamentum mandibulo-hyoideum externum.
lgt. m-h. i. Ligamentum mandibulo-hyoideum internum.
mem. Membrane.
n. c. Nasal capsule.
oc. cond. Occipital condyle.
pc. Procoracoid.
p. sc. Posterior semicircular canal.
pub. is. Pubo-ischium.
r. Raphe.
ra. Radiale.
r. p. Rostral process.
sc. Scapula [cartilaginous].
s-o. a. Supra-occipital arch.
s. r. Sacral rib.
t., 1–5. Tarsals 1–5.
tib. Tibiale.
tq. Trabeculo-quadrate isthmus.
tr. Trochanter.
trab. Trabeculum.
uln. Ulnare.

PLATE 2.

Fig. 1. Dorsal view of skull; left nasal capsule and left half of mandible removed. × 6.
Fig. 2. Ventral view of skull; mandible removed. × 6.
Fig. 3. Lateral view of skull; mandible attached. × 6.
Fig. 4. Mandible from above. × 6.
Fig. 5. Pelvis; ventral view. × 6.
Fig. 6. Pelvis; dorsal view. × 6.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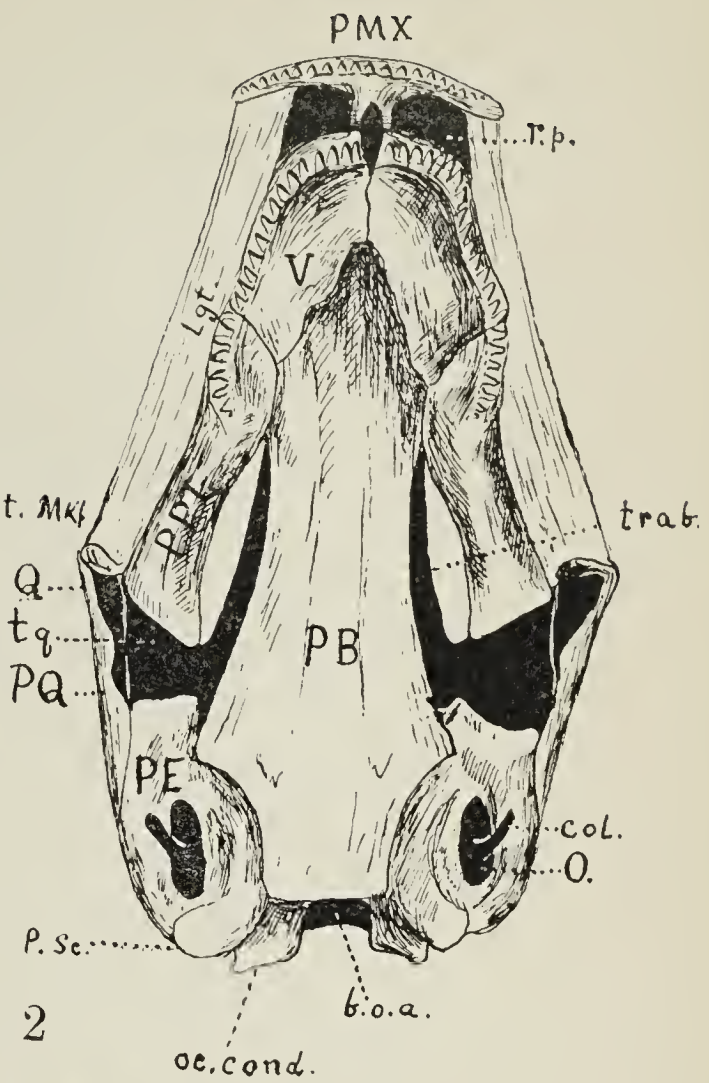
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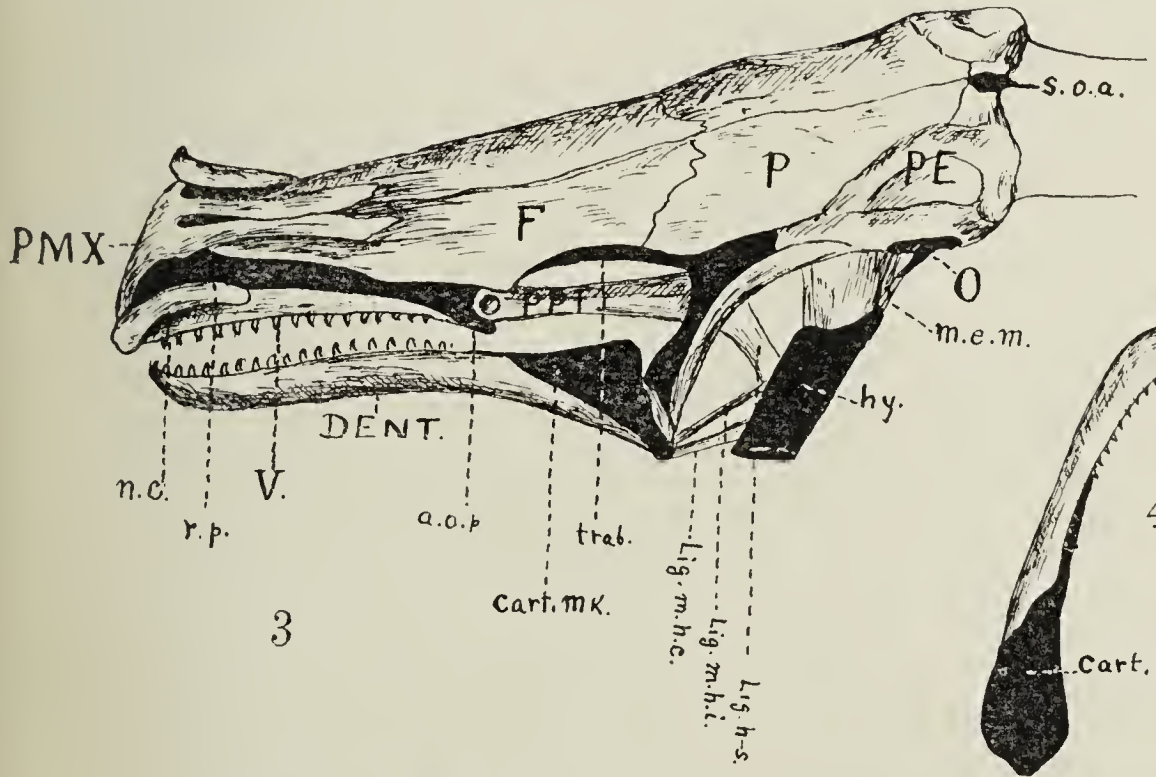
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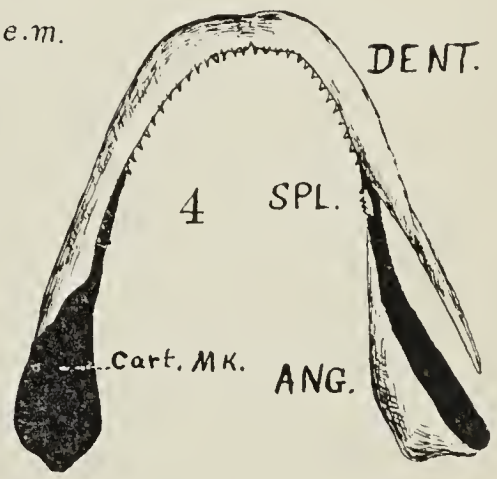
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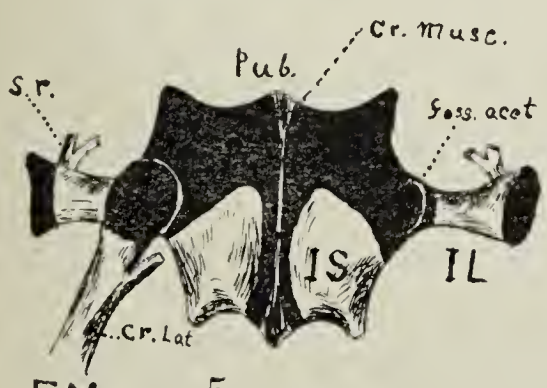
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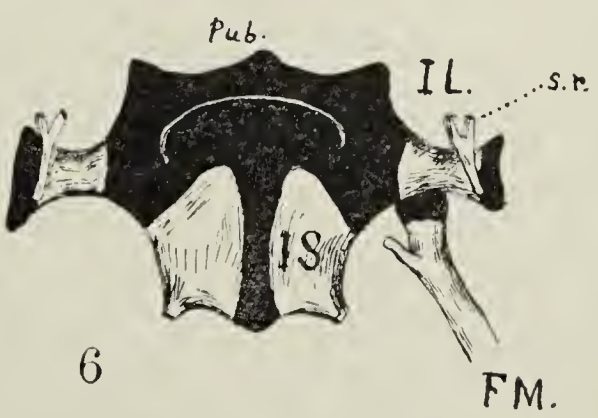
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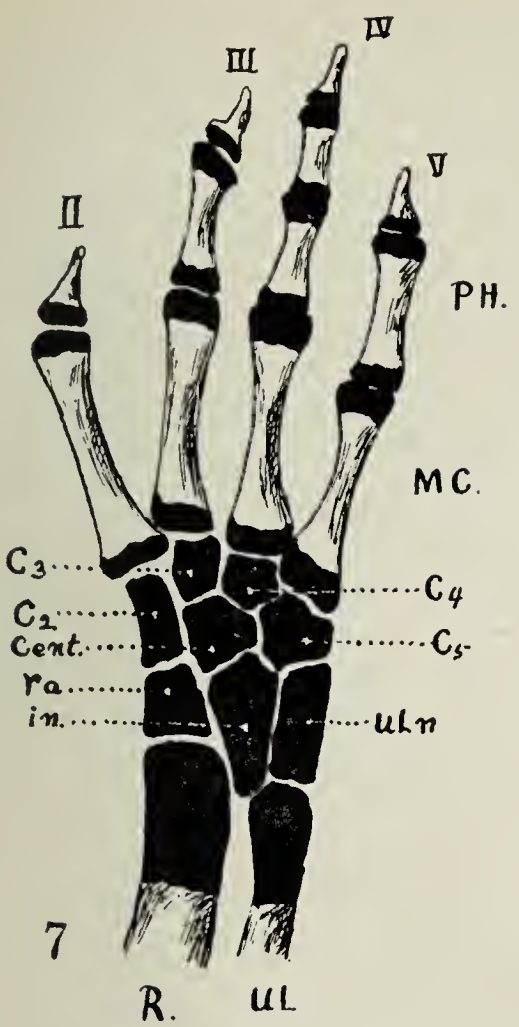
PLATE 3.

Fig. 7. Right manus ; dorsal view. × 12.
Fig. 8. Right pes ; palmar view. × 12.
Fig. 9. Right half of shoulder girdle and right fore limb; outer surface. × 6.
Fig. 10. Right hind limb ; inner surface. × 6.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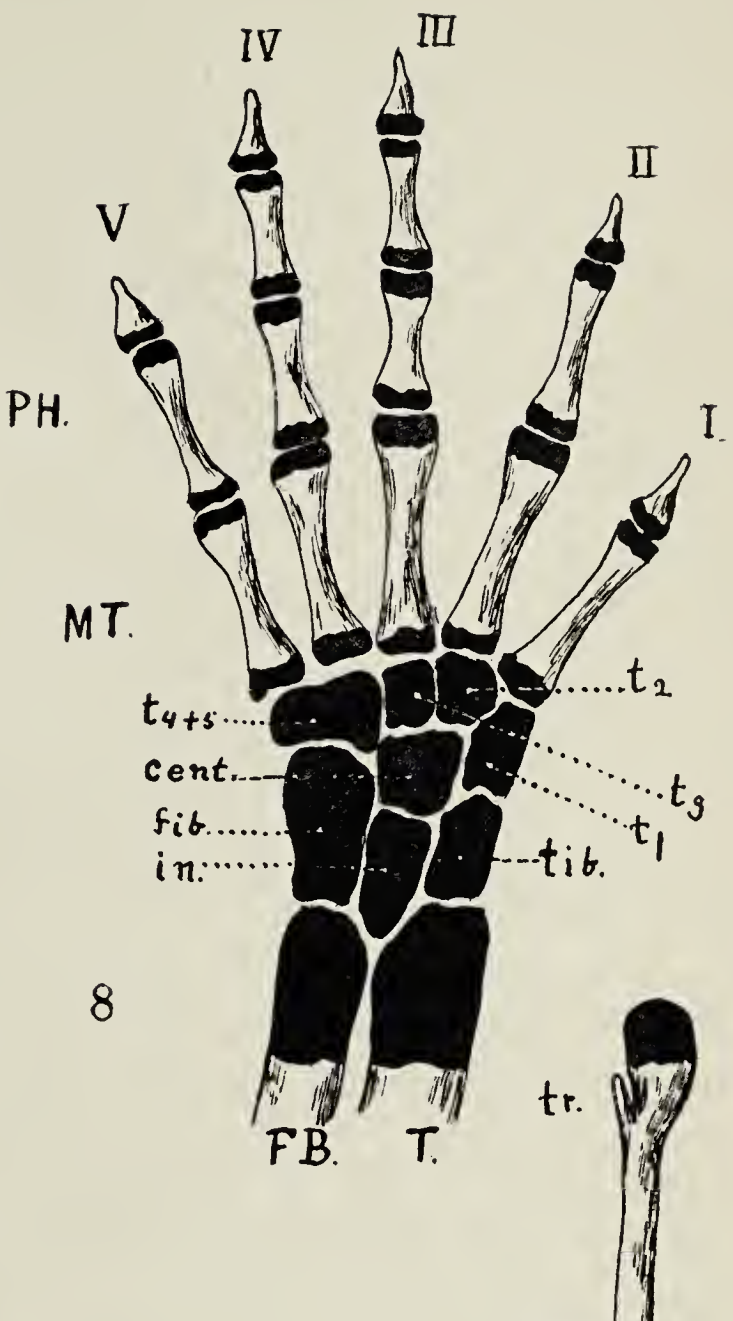
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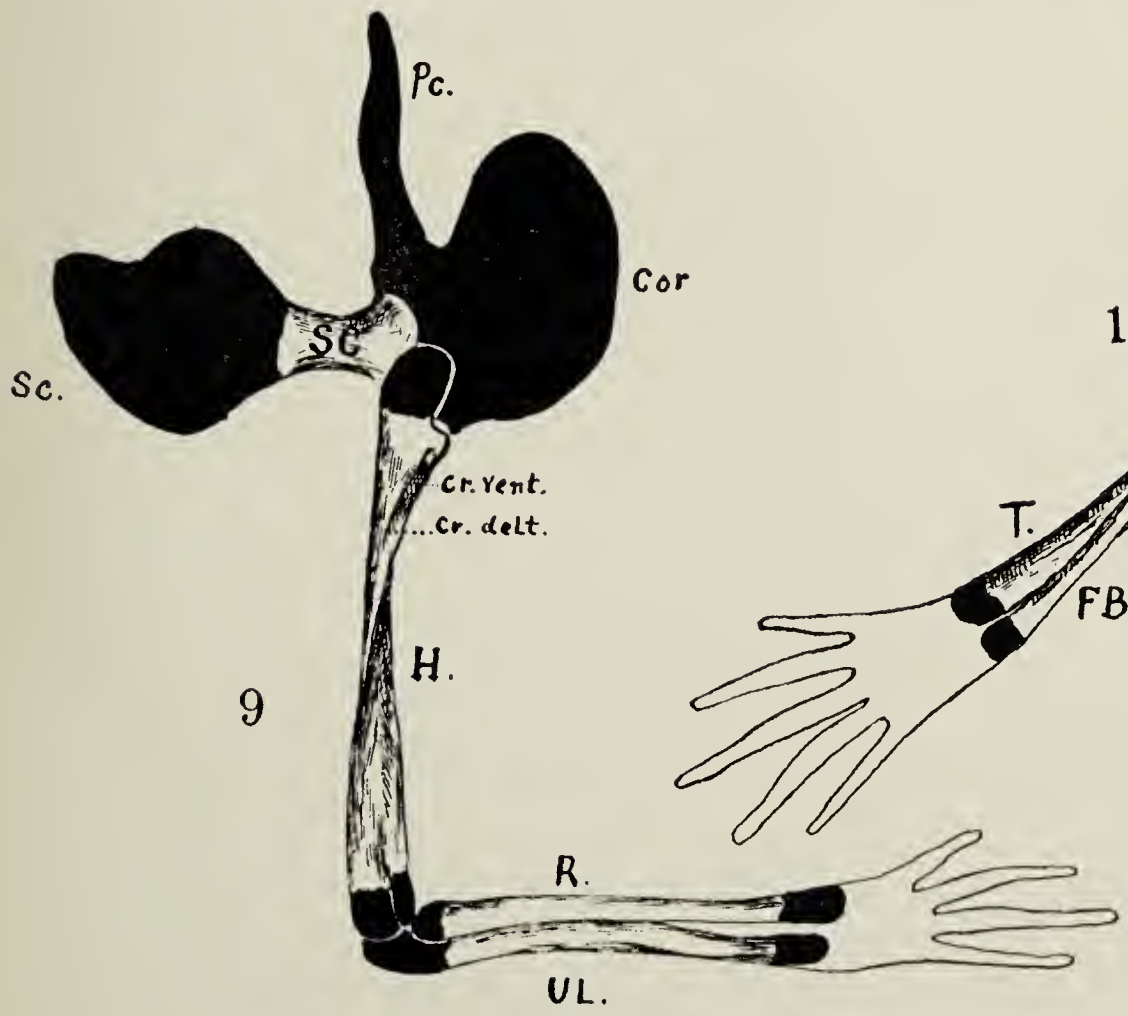
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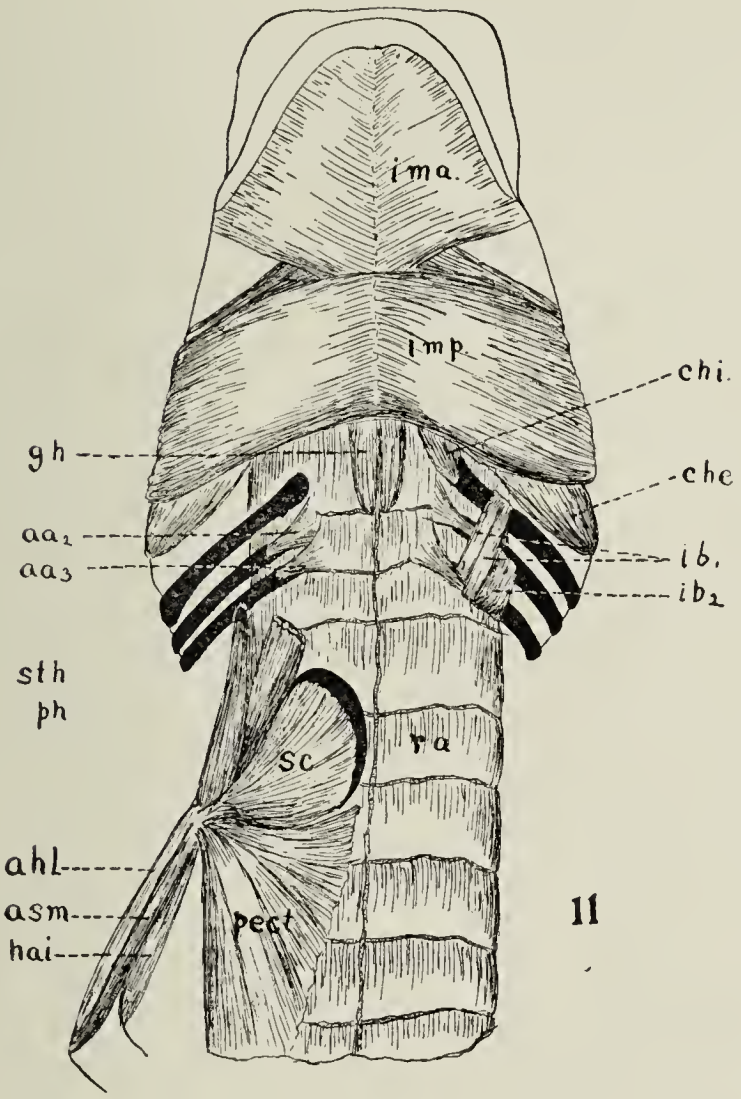
PLATE 4.

Fig. 11. Muscles of the head; ventral view. × 3.
Fig. 12. Muscles of the head; dorsal view. × 3.
Fig. 13. Muscles of the head; lateral view. × 3.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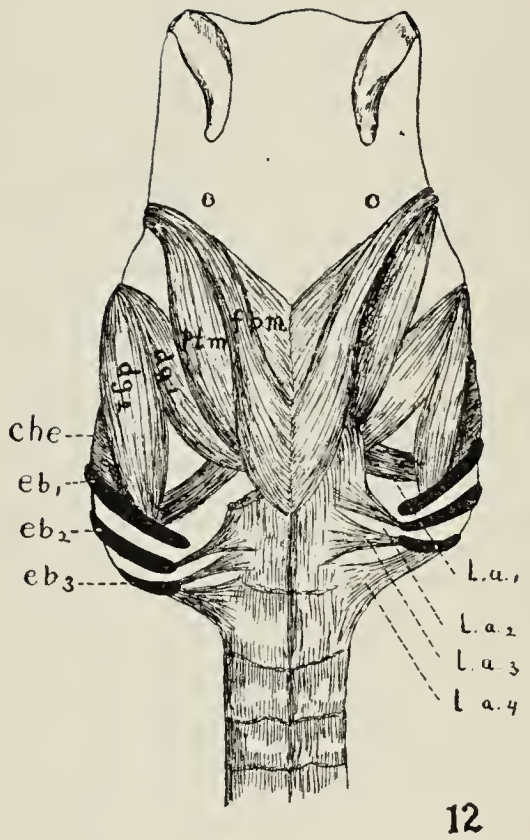
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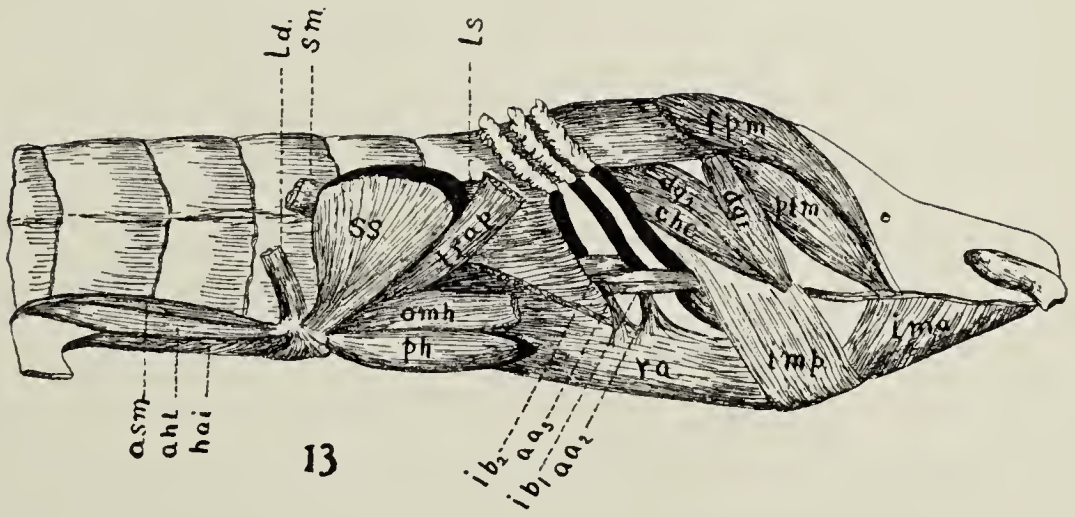
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PLATE 5.

Fig. 14. Hyo-branchial apparatus; pharyngeal aspect. × 6.
Fig. 15. Hyo-branchial apparatus; ventral view. × 6.

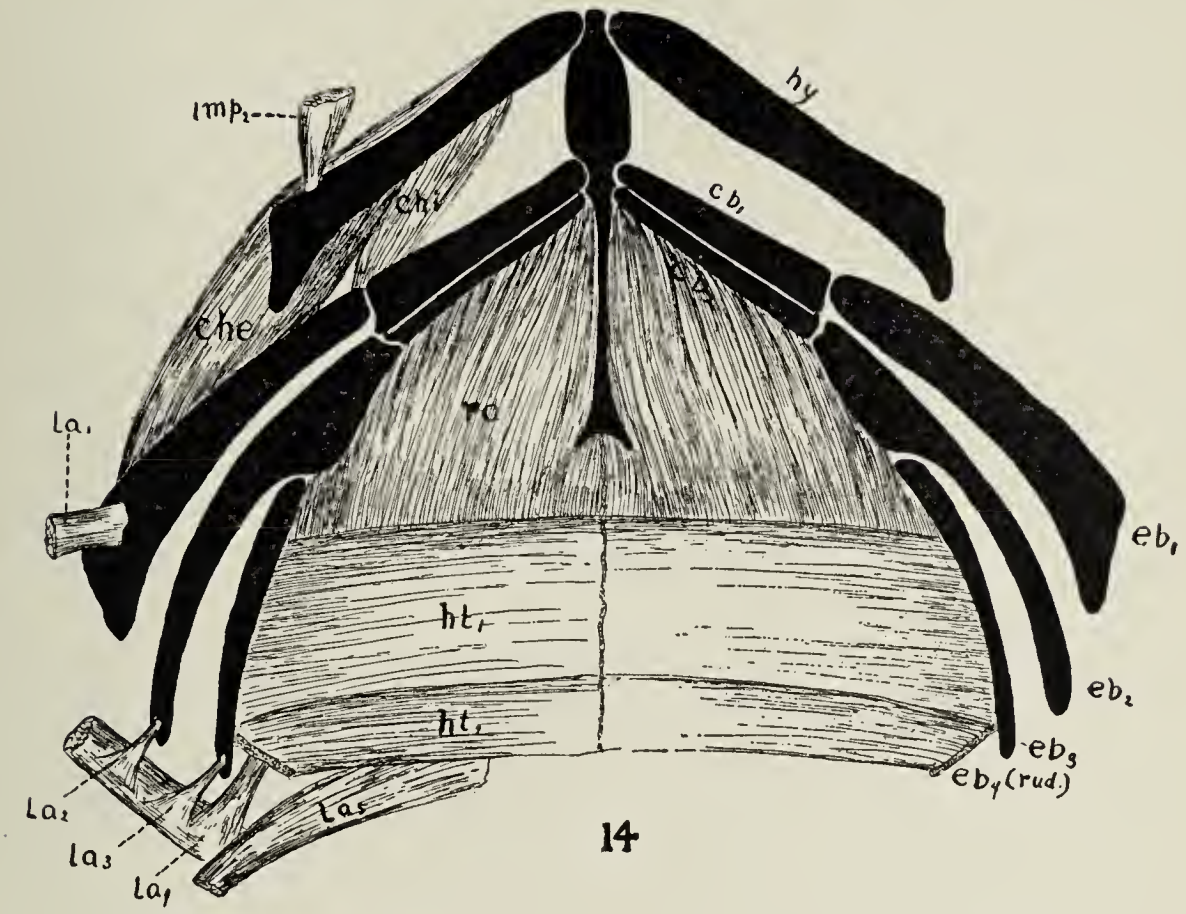
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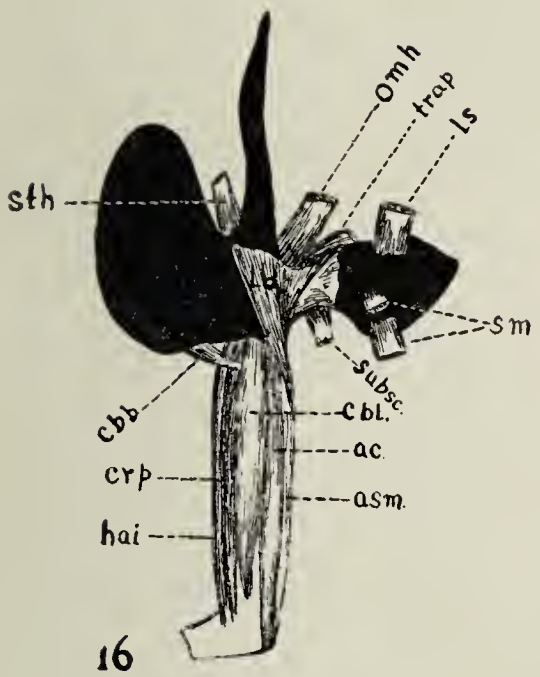
PLATE 6.

Fig. 16. Muscles of fore limb ; inner surface. × 4.
Fig. 17. Muscles of hind limb, superficial layer ; ventral view. × 3.
Fig. 18. Muscles of hind limb, deep layer ; ventral view. × 3.
Fig. 19. Muscles of hind limb ; dorsal view. × 3.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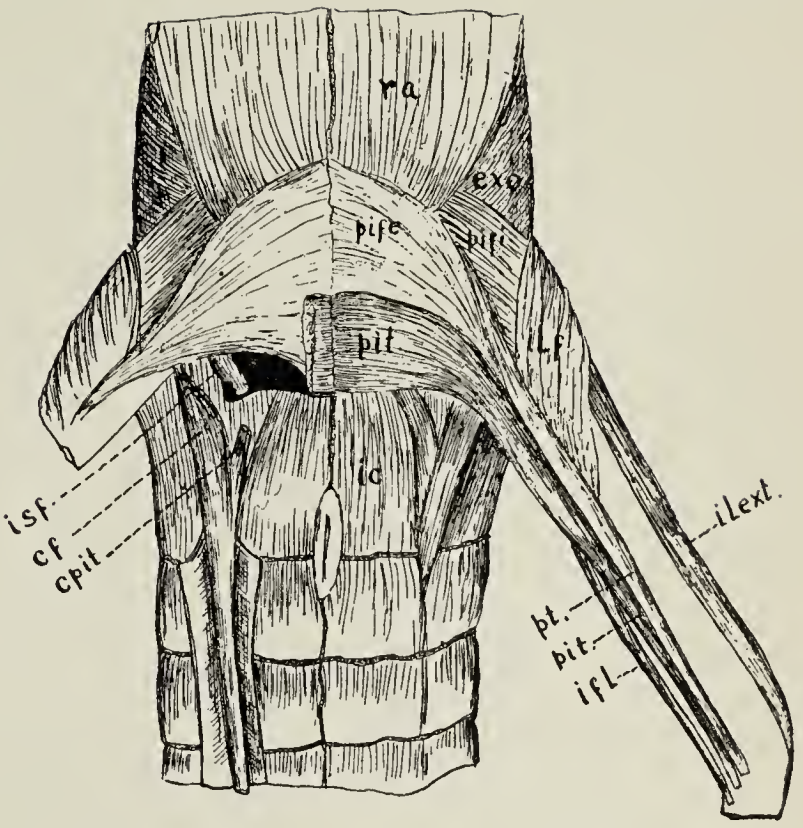
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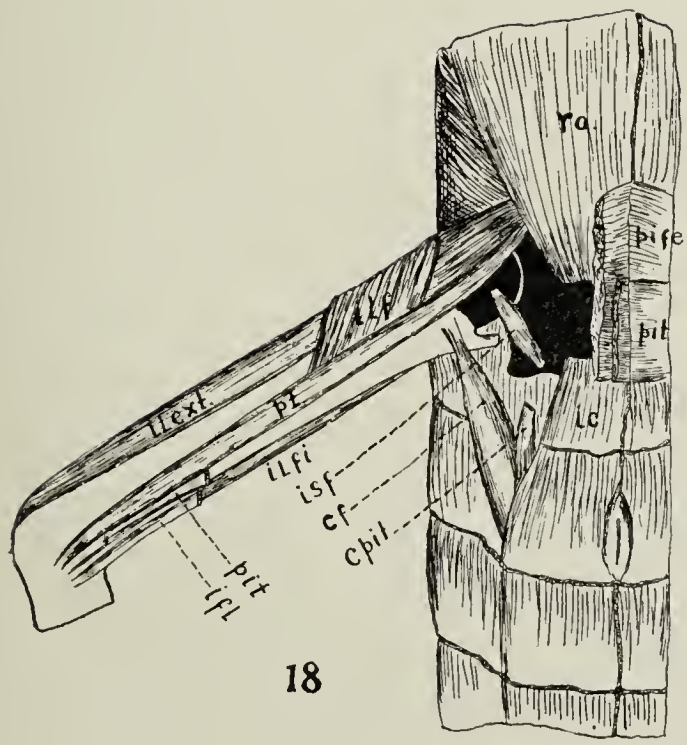
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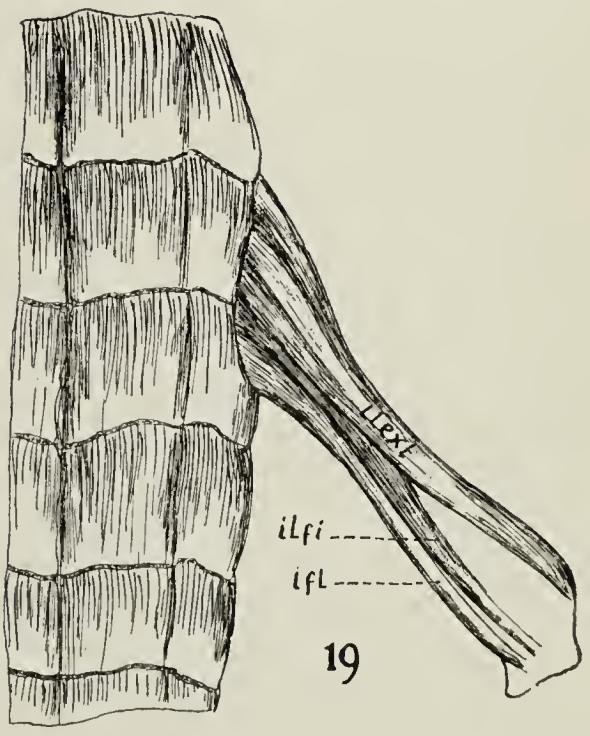
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Proceedings of the Boston Society of Natural History.

Vol. 32, No. 4,

p. 77–113, pl. 7–11.

DEVELOPMENT OF ASCUS AND SPORE FORMATION IN ASCOMYCETES.

By J. Horace Faull.

BOSTON:

PRINTED FOR THE SOCIETY.

June, 1905.

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No. 4. — DEVELOPMENT OF ASCUS AND SPORE FORMATION IN ASCOMYCETES.[1]

BY J. HORACE FAULL.

De Bary ('63, '84) was the first contributor to our knowledge of the cytology of the ascus. His investigations showed that the comparatively young ascus was uninucleate and that it continued to be so until its maximum size was reached; that three successive nuclear divisions followed; that simultaneously about each of the eight resultant nuclei there gathered a rounded mass of protoplasm differing from the surrounding protoplasm, the epiplasm, by its greater transparency, and bounded off from the latter by a delicate line; and finally that these spore initials acquired an exospore and matured at the expense of the epiplasm.

Strasburger ('80) and Schmitz confirmed De Bary's observations in a number of forms, and Gjurasin ('93) not only did the same in *Peziza vesiculosa* Bull., but by the aid of a more modern technique followed with much greater minuteness the processes within the ascus. Gjurasin discovered that the nuclear divisions were karyokinetic, that there were well marked asters, though centrosomes could not be demonstrated, that the anaphase stage was reached before the nuclear wall disappeared, and that the nucleolus remained until the daughter nuclei were formed. Of greatest interest were his observations on the last nuclear division. The third set, unlike the first two sets of spindles, was placed with the long axes at right angles to the long axis of the cell. The asters of this generation persisted much later than those of the two former. During the final stages of division the spindles elongated considerably, bringing the asters near the wall of the ascus. He figured the rays as continuing in the same position as when attached to the spindles, though disconnected from the nuclei and folded inwards over the latter like the ribs of an opened umbrella.

Dangeard's ('94) attention was fixed on the young ascus. He described the origin of the asci in *Peziza vesiculosa*, *Borrera ciliaris*, and some two or three other forms. The first indication of the

[1] Contributions from the Cryptogamic laboratory of Harvard university.— LXI.

JUN 26 1905

advent of an ascus according to this investigator, was the appearance of four nuclei in a recurved tip of an ascogenous hypha. Next, by means of transversely placed walls, these nuclei were separated from one another so that one lay in the end, two in the second cell, the curved portion of the hypha, and the fourth in the third cell. The ascus grew out from the second cell, the two nuclei of which fused, resulting in a uninucleate condition of the ascus, the earliest stage observed by De Bary. Dangeard at first maintained that the ascus grew out from the point of junction of two hyphal threads, which he supposed to be male and female organs respectively. Subsequently he discovered that there was no such fusion, but that the phenomena are such as I have just described.

Harper (:00) has verified Dangeard's observations in *Pyronema confluens*. He has shown further that there are at first two nuclei in the recurved tip of an ascogenous hypha, that these divide mitotically and synchronously to form the four observed by Dangeard, and that one of each pair of daughter nuclei is relegated to the young ascus. Harper has also confirmed the work of Gjurasin, but his most important work began where Gjurasin's left off. His main problem has been to determine the exact process involved in the delimitation of the plasma of each spore. He has investigated the origin of the spores in *Erysiphe communis*, *Peziza vesiculosa*, *Ascobolus furfuraceus* (Harper, '97) *Lachnea scutellata* (Harper, '99), and *Pyronema confluens* (Harper, :00), and has concluded that the process is practically the same for all of the Ascomycetes.

According to Harper this process is a distinctly unique one. The first step consists in the formation of a beak by each nucleus. This beak bears at its extremity the persistent centrosome and astral rays. The astral rays next swing outwards and down, the uppermost coming into contact laterally and fusing into a thin membrane. At this stage as far as relative positions are concerned, the membrane bears the same relation to the nuclear beak that the cover of an opened umbrella does to the rod that supports it. This "kinoplasmic" membrane continues to grow downward. Eventually it curves inward, the edges meet at a focal point, and the process of delimitation is complete. There has been no aggregation of protoplasm about the nucleus, but the membrane of fused astral rays, the plasma membrane of the young spore, literally cuts the spore plasma out of a homogeneous mass of protoplasm.

Berlese ('99) investigated the sporogenesis of *Tuber brumale*. His results in the main corroborated those obtained by Gjurasin and Harper. He expressed the opinion that the astral rays determine the formation of the plasma membrane of the young spore.

The only other work to be noted in this connection is that of Errera and Guilliermond. Errera ('82) demonstrated for the first time the presence of glycogen in the epiplasm. It occurs in a semi-fluid, amorphous, strongly refractive form, the reactions of which are identical with those of animal glycogen and the function of which is likewise taken to be nutritive. Guilliermond (:03, :03b) has recently pointed out the presence of certain granules in the asci of *Ascobolus marginatus*, the Aleurieae, the Helvellineae, etc., and in the spores of *Peziza coccinea*, which he, too, considers to be reserve matter, the same as the "corpuscules métachromatiques" or "granulations basophyles" described by him (:02) in the yeasts and moulds, and very like, if not the same as, Bütschli's "grains rouges" and Babe's "corpuscules métachromatiques" found by them in bacteria and the Cyanophyceae.

From the foregoing it is quite evident that the origin and cytology of the ascus are known in but a small number of forms, and on these are based generalizations for the entire group. Briefly, it is considered that the ascus is an outgrowth of the penultimate cell of the recurved tip of an ascogenous hypha, that it at first contains two nuclei which later on fuse, that there follows a series of mitotic divisions, that finally the spores are cut out of a homogeneous plasma by a membrane formed by the fusion of the astral rays of the last generation of nuclei, and that the growing spores are nourished by a food supply which is, at least partly, in the form of glycogen and an unknown substance, the "corpuscules métachromatiques."

The investigations, the results of which are presented in this paper, were undertaken in the hope of extending our knowledge of the ascus to a number of forms hitherto unexamined. A wider knowledge especially of the earlier stages in the development of the ascus and of the immediate details in the forming of the spores seems desirable because of the light that may be shed not only on the question of the affinities of the Ascomycetes among themselves, but also on the larger question of the affinities of the group as a whole.

Probably the most favorable forms that have come under observa-

tion have been *Sordaria fimicola*, *Neotiella albocincta*, and Hydnobolites.

Most of the material was gathered out-of-doors, but the Sordarias and the Podosporas were taken from pure cultures. Several species of Sordaria and Podospora are readily obtainable from horse- or cow-dung brought into the laboratory and kept moist. Pure cultures of any particular species can then be secured by carefully transferring to sterilized dung or other suitable soil, or by catching the spores on a glass slide and sowing them. The objection to dung as a substratum is that it contains sand and small pieces of straw, some of which are sure to adhere to the preserved material and so interfere with cutting. This difficulty was avoided by using green string-beans or dung covered by a thin layer of ground sphagnum moss, on both of which nearly as abundant crops can be grown as on the normal substratum.

Sordaria fimicola was the most serviceable of all the Sordariaceae examined. It is one of the commonest of coprophilous fungi and lends itself to cultivation particularly well. Moreover it matures within a week or ten days after the spores are sown. Further, the perithecial wall is thin and so fixation with such reagents as Flemming's weaker solution is possible, the nuclei are comparatively large, and the ascus is not loaded up with a great deal of diffused reserve matter. Material of *Sordaria fimicola* was preserved at nearly every hour of both the day and the night, but it was found that the various phases in the development of the asci may occur at any time if the proper conditions of temperature prevail. Most of the Podosporas are difficult of fixation. Experiments were made in snipping off the pointed ends of their perithecia with fine scissors, but the results were rather indifferent.

Several species of wood fungi were examined, such as *Massaria vomitoria*, *Massaria platani*, *Propolis faginea*, many of which were gathered in February and March. The most promising of these were the Massarias.

It is worthy of note in this connection, that the apothecium of *Urnula craterium* is well started in the autumn, although the asci do not make their appearance until the following spring. While collecting in November, 1901, in the neighborhood of Bedford, Mass., a number of specimens were found on the underside of oak sticks lying on the ground. They looked like giant Podosporas,

though much lighter in color, and were protected by a hirsute covering. Some had attained a height of 2 cm., and a diameter of 0.6 cm. Several were marked, and placed under further observation. It was found that they matured rather slowly in the spring, for they were not ready to shed their spores until the early part of May.

Several fixing fluids were used, but Flemming's weaker solution was found to be the most satisfactory. Likewise several stains were tried, but Flemming's triple stain of saffranin, gentian violet, and orange G, and Haidenhain's iron-haematoxylin were found to be superior to all others. No hard and fast rule can be laid down for staining. Nearly every species requires a somewhat special treatment. Material for cutting was embedded in paraffin whose melting point was about 57° C. and sections were cut from 3 μ to 5 μ in thickness. In determining the origin of the ascus it was frequently of advantage to crush slices of fresh or preserved material, preferably the latter, and examine in water or potash. Figures 70 to 80 (pl. 11) were drawn from preparations made in this way.

Hydnobolites sp.

Within the bounds of a brief paragraph, Errera ('82) recorded the fact that the spores of Tuber are formed simultaneously and not successively, as was formerly believed, that at the moment of their birth they are surrounded by a thin membrane, and that the rest of the protoplasm in the ascus condenses about them to form the greater part of the exospore. Berlese ('99) has recently given us a much fuller and more accurate account of the phenomena that occur within the ascus of *Tuber brumale*. Hydnobolites as far as I am aware is the only other hypogeous Ascomycete that has been examined from a modern cytological standpoint. I owe the material to the kindness of Professor Thaxter, who gathered it at Kittery Point, Maine, in September, 1903.

Hydnobolites is admirably adapted to a cytological study. The fruits can be readily cut into thin sections, and each section contains two or three score of asci in all stages of development. The asci are comparatively large, and owing to their spherical shape and the disposition of the spore-forming plasm do not suffer from being cut in any plane. *Tuber dryophyllum* was also examined, but not as fully, for its structural features are on a smaller scale. There is

likewise more objectionable reserve matter in the way, and very few spores are found in an ascus.

The ascus in Hydnobolites springs from the penultimate or terminal cell of the tip of an ascogenous hypha (pl. 11, fig. 78), so that in this respect it may depart from the conventional type. From the first it has the spherical form. In the early stages its protoplasm is granular and irregularly vacuolated throughout, but little attention was paid to the nuclear or other phenomena belonging to this period.

The condition represented in figure 1 (pl. 7) was taken as the starting point for a more careful examination. At this stage there is a very distinct differentiation of the cytoplasm. The greater part of the ascus is occupied by large vacuoles that are filled mainly with watery sap, while there is a small mass of thick protoplasm in the upper part of the sac, against the wall or removed but a short distance from it. Viewed from above, this mass is seen to be of a discoid form, and viewed laterally of a somewhat lenticular shape (pl. 7, figs. 2, 3). A large nucleus lies in the center or along the lower border of the thick protoplasm. It is limited by a clearly definable membrane, possesses a comparatively large nucleolus, and contains a very small amount of chromatin. The last is arranged in the form of fine granules on a filar achromatic network, but the nuclear sap has such an affinity for stains that these features are often almost obscured.

Outside of the nuclear wall at about this time and closely in contact with it there appear small granules that stain a bright red with Flemming's triple, and black with iron-haematoxylin. These granulations have been observed elsewhere and are probably the same as Guilliermond's (: 02) "corpuscules métachromatiques." That they are not artifacts as Harper ('99) supposed for similar appearances in *Lachnea scutellata* is very obvious from the fact of their constant occurrence and rather characteristic features at different stages.

Both the nucleus and the dense protoplasmic mass increase in size, the latter frequently passing through a vacuolated condition as represented in figure 2 (pl. 7), while the extranuclear bodies tend to become fewer and larger. This vacuolated condition is succeeded by one (pl. 7, fig. 3) in which the protoplasm is finely granular, though marked by coarse strands that tend to radiate from the nucleus. The latter is still surrounded by the granules or extra-

nuclear bodies, which have apparently increased in number. These granules very soon move away from the nucleus. At first they are scattered throughout the protoplasmic mass (pl. 7, fig. 4) but eventually pass to its periphery (pl. 7, fig. 5). Soon after the first spindle stage they almost entirely disappear.

In the meantime the protoplasm has been undergoing changes. Simultaneously with the dispersion of the extranuclear bodies the protoplasm in the neighborhood of the nucleus becomes hyaline and more finely reticulated. This hyaline protoplasm possesses a radiate structure with the nucleus as a center (pl. 7, fig. 4). These changes are indications that the first nuclear division is near at hand. The transforming process is extended to all of the dense protoplasm, except a coarsely and irregularly reticulated sheath at the periphery, in which the red granules have come to lie. At this stage a centrosome and aster make their appearance, as shown in figure 5 (pl. 7) in a tangential plane that is parallel to the long axis of the spindle that is to follow. The steps leading up to the formation of the spindle were not determined.

The first spindle (pl. 7, fig. 6–13) is generally not as striking as those of the two succeeding generations. It is intranuclear, a condition that lasts until a comparatively late anaphase stage, generally eccentrically placed and terminated by centrosomes from which radiate long rays into the surrounding protoplasm. The rays are very coarse and long and are readily demonstrable with either the triple stain or with the iron-haematoxylin. It is worth noting that they stain differently from the centrosome. They are connected with the centrosome but that they are outgrowths of this body is open to question. Again there is no more evidence that they are retracted to the centrosome at the time of their disappearance, as has been suggested, than that they originated therefrom. Indeed, instead of being resorbed by the centrosome they appear to fade out in the cytoplasm. Moreover, since the latter changes so constantly, as we have seen, it is not difficult to believe that the astral rays are cytoplasmic modifications.

It has further been suggested (Harper, '97) that in *Erysiphe communis* the number of astral rays may be the same as the number of spindle threads and continuous with them. Their existence previous to the appearance of the spindle, their separation from the spindle by centrosomes of even earlier existence than their own, and

both an apparent disparity in their number and that of the spindle threads, and the unlikelihood of the tenuous threads of the spindle fusing through the centrosome with the coarse rays, argue against any such relation between spindle threads and astral rays in Hydnobolites.

Throughout the division of the nucleus the centrosome appears to be considerably augmented by a granular mass. Both the solid and the granular parts are shown in figure 7 (pl. 7). It is likely that the granular portion consists in part of bases of rays lying in other planes than in the one represented in the drawings.

The chromosomes are very small and are four or five in number. The daughter chromosomes separate after cleavage, and on reaching the terminals of the spindle the latter begins to elongate. The result of this is that the nuclear wall is distorted (pl. 7, fig. 10) Finally the nuclear wall disappears, leaving both spindle and nucleolus in the cytoplasm. The spindle threads elongate still farther before their disappearance, the chromosomes in the meantime losing their identity and passing into a tight clue condition (pl. 7, fig. 13). Eventually the astral rays are no longer visible, new walls are formed about the nuclei, each centrosome shows as a small solid mass in a position 90° removed from its position during the division of the mother nucleus, the chromatin again forms a network and each nucleus acquires a nucleolus (pl. 7, fig. 14). The old nucleolus begins to appreciably diminish during the anaphase stages of the division. Its disappearance does not keep step with the development of nucleoli in the daughter nuclei as Gjurasin ('93) thought to be the case in *Peziza vesiculosa*. Another noticeable feature is that the cytoplasm does not now seem to be differentiated as it was during and just prior to the division of the nucleus, and has become rather coarsely reticulated (pl. 7, fig. 14).

After a short period of rest the division of the two daughter nuclei is initiated by the same differentiation in the protoplasm surrounding them that was observed just before the first division. The protoplasm becomes finely reticulated and presents a radially striate appearance (pl. 7, fig. 15). As before, the change in the surrounding protoplasm extends almost to the limits of the dense cytoplasm. The prophase stages are identical with those already observed. It may be noted in this connection that the centrosomes are frequently not demonstrable during the resting periods between the first and

second and between the second and third spindle stages. But they either reappear or else are formed anew in the early prophase stages of mitosis.

The spindles of this generation lie in about the same plane as that in which the first lay, and end to end in a straight line. They are more easily studied than was the first, and though not different from it in the main, yet exhibit certain peculiarities that readily distinguish them. Thus, unlike the first, they occupy a proportionately larger part of the space within the nuclear wall, they are not eccentrically placed, their astral rays are somewhat coarser, and there is a sort of mantle formed about the intranuclear part of each (pl. 7, fig. 16). This mantle, the definite character of which was not determined, adheres to the middle part of the spindle for some time after the nuclear wall goes to pieces. In all probability it is not a mantle of fibers belonging to the spindle, for figure 17 (pl. 8) indicates that there is no connection with the centrosomes. In the anaphase stages the spindle elongates, at first giving to the nuclear wall an oval shape, and after the disappearance of the latter, still continues to extend. The stretching or growth of the fibers, whichever it may be, is the most pronounced in this case of all the three mitoses occurring within the ascus. Finally, the threads of the spindles vanish, and the four daughter nuclei form, and pass into a resting condition, as we saw for the nuclei that preceded them. They change their relative positions, however, so that, while in practically the same plane, they are not in a straight line.

Coming now to the last mitosis it is to be noted that the phenomena up to the anaphase stages are the same as have been described for the second division, and they are as readily observable. The spindles may lie side by side or at an angle to one another, but all are in about the same plane (pl. 8, fig. 19). Interest centers in the events subsequent to the spindle stage, for before the daughter nuclei reach the resting state the young spores are delimited.

We have already seen that one of the features of the anaphase stages of the first two mitoses is an elongation of the spindle fibers. The same is true of the third. The result of this elongation in the last case is to bring the young daughter nuclei against or near the upper part of the plasma membrane that surrounds the dense protoplasm. Thus in looking down on the upper end of the ascus as represented in figure 21 (pl. 8) the centrosomes of five nuclei could

be seen in the same field. Presumably the causes of elongation in this case are the same as in the preceding ones. There is no evidence to show that some of the astral rays become attached to the plasma membrane and then contract, thereby drawing the nucleus up against the membrane.

Another striking anaphase condition is the persistence of the asters after the spindle fibers have disappeared. But this happens with the last generation of daughter nuclei only. They persist until the young spores are formed. This naturally leads us to enquire what part, if any, the astral rays play in spore delimitation.

This question has been investigated by Harper ('97) in a number of forms of which *Erysiphe communis* was apparently best suited for the purpose. His answer in a word was that the astral rays effect the separation of the spore plasma from the surrounding protoplasm by forming the limiting membrane or plasma membrane of the young spore. He states that the eight nuclei of the third generation lie irregularly arranged in the ascus, each with its centrosome and polar rays. A beak then appears on each nucleus on the end of which is the aster. This beak is about equal in length to the diameter of the nucleus and is a small tube sometimes with an expanded top. Into this tube the chromatin network extends. His assumption was that this last fact seemed to prove that there was a union between the chromatin and the centrosome. He regarded the beak as a growth and not as being produced by a pulling out of a side of the nuclear wall. He noted that the beaks were turned toward the ascus wall. As soon as (*before*, according to his figures) the beaks had reached their maximum length, the polar rays experienced a remarkable transformation. The rays began to turn outward, and in moving outward came into contact laterally and fused into a membrane. At this time the membrane formed a funnel or inverted hollow cone the apex of which was at the centrosome. The rays constituting the membrane now began to grow rapidly in length and at the same time to bend down toward the nucleus. The membrane cut through the protoplasm and finally its edges met at a point opposite the centrosome. This completed the process of delimitation and at the same time furnished the spore with a plasma membrane.

Turning now to Hydnobolites we find that the phenomena presented there are apparently quite different. We have already

observed that the eight nuclei of the last generation lie in close proximity to the plasma membrane surrounding the thick protoplasm. As yet their walls are unformed and chromatin and centrosome are indistinguishable. The astral rays are long and prominent, but except for a different position from that represented in figure 19 (pl. 8) they are unchanged. Figure 21 (pl. 8) presents a view of the condition of affairs at this time in polar view, and figure 23 (pl. 8) of perhaps a slightly later stage. From these figures it is evident that the rays have now come to lie in a plane that is nearly parallel to the plasma membrane, that is, in a plane which stands at an angle of 90° to that in which they lay in the equatorial stage of the spindle. Indeed, they are slightly bent down towards the nucleus, a bending that becomes more and more accentuated. The writer, however, dissents from the view (Harper, '97) that the rays are moving down to become the plasma membrane of the spores and that their movements are comparable to the movements of the cilia of zoospores.

Changes in their position might be explained in part by two causes: (1) the outward movement of the nuclei. Thus there is a similar though not as extensive spreading movement of the rays at the end of the first and second mitoses (compare with fig. 12, pl. 7 and fig. 17, pl. 8). (2) Further, if the centrosome be a dynamic center and the rays an expression of cytoplasmic activity controlled by the nucleus, then they would change their position at this time, for now the bulk of the cytoplasm lies centrad of the centrosome, and it is here that aggregation and differentiation of spore plasm is taking place.

It is not impossible that some of the rays pass into the plasma membrane surrounding the dense protoplasm as Harper ('99) has suggested for *Lachnea scutellata*. Cases have been observed in which the rays seem either to stop short at the membrane or to be absorbed by it, but generally they bend away. The same investigator (Harper, '97) corroborates this last observation in the figures accompanying his paper on Erysiphe. Moreover, a reference to figures 11 and 16 (pl. 7) of this paper shows that the development of the rays on the membrane side is less than on the side in which the bulk of the protoplasm lies.

Figures 23, 24, and 25 (pl. 8) represent the next stage, the one in which delimitation of the spore begins. This process is initiated by

the formation of a specialized layer of protoplasm, perhaps of the same nature and formed in the same way as the hyaline zones observed by Harper ('99) in Pilobolus. This layer begins just outside the centrosome and is formed progressively from that point until it encloses the plasma of the future spore. In figure 24 (pl. 8) it is not yet half completed. It is very thin at first, but gradually thickens and since it stains differently from the rest of the protoplasm, is quite clearly definable. That this limiting layer of protoplasm is a membrane, however, is very doubtful, and that it is composed of fused astral rays is contrary to my observations.

That the astral rays do not fuse is readily demonstrable in Hydnobolites. They are very long during the spindle stage, and do not materially alter in length after that. They do change their position, it is true, but the change is one that throws them farther apart instead of bringing them closer together. Fusion is, therefore, a physical impossibility. The only way in which fusion could be effected would be by the flattening of the rays, or by a growth of lateral wings on each. But a polar view at this or any other stage presents no such transformations. The rays are distinct and unchanged, and the limiting layer is of uniform thickness. Indeed, it is quite obvious that whatever the composition of the limiting layer may be, it does not consist of fused astral rays.

While the spore plasma is being separated in this way, it is observable that a change is taking place in its structure. Starting from the nucleus the protoplasm that is to be included within the spore becomes more finely reticulated and eventually more hyaline than that outside. Such a change suggests that there may be a connection between the refining or differentiation of the spore plasm and the formation of the limiting layer.

About the time the limiting layer is being constructed, the nuclear wall is formed. When the completed nucleus is first demonstrable, it presents the appearance of a short cylindrical vesicle. It then elongates, growing towards the center of the spore mass, or to one side or the other at any angle (pl. 8, figs. 26, 27). Meanwhile it retains its cylindrical shape. Eventually it grows beyond the middle of the spore, so that its length may be equal to three quarters the diameter of the spore. Likewise it becomes bottle- or flask-shaped, the neck becoming quite tenuous (pl. 8, figs. 29, 32). But this "beaked" shape is not evident until long after the spore is delimited.

The early elongation of the nucleus is undoubtedly accompanied by growth. It may be that, in addition to this, there is a tension brought to bear on the nucleus, a tension that may have its origin outside of the spore altogether (pl. 8, figs. 29, 32). That the bottle- or beak-shape is the result of a pull on the nucleus is rather more obvious, for there is an elongation without an appreciable increase in volume. Nevertheless this bottle-shape might be brought about through other changes, such for instance as the transfer of the chromatin and nuclear sap to the distal end of the nucleus, and the consequent shrinking of the proximal end. If there be a pull, however, it is not strong enough to pull the centrosome away from the delimiting layer of protoplasm. Indeed the centrosome does not sever its connection with the periphery of the spore mass until after the plasma membrane of the spore is constructed.

The formation of the plasma membrane of the spore is subsequent to that of the limiting layer of protoplasm already noted, although it may begin before the latter is completed. Figures 26 to 30 (pl. 8) represent this membrane in various stages of growth. In figure 26 (pl. 8), only one of the poles of the spore is covered while in figure 29 (pl. 8), the membrane is all but finished. Figure 33 (pl. 8) is a polar view of about the stage represented in figure 29 (pl. 8).

Concurrently with the formation of the plasma membrane of the spore, another is formed in contact with it. This second membrane lines the cavity in which the young spore lies. Both occupy the site of the limiting layer of protoplasm, and along this their line of development follows. The development of these membranes is progressive, beginning at a point contiguous to the centrosome and continuing until the opposite pole of the spore is reached. To just what extent the substance of the limiting layer enters into the composition of these membranes, it is rather difficult to say. Nor is it clear that their formation is preceded by a change in the limiting layer. It is certain, however, that the membranes are separable and a cleavage between them can be observed under favorable circumstances up to the limits of their construction. Observation is rendered especially easy in case there has been a slight shrinkage or inequality in fixation (pl. 8, figs. 29, 33).

In regard to the relation between the plasma membranes and their precursor, the limiting layer, it is highly probable that the development of the former is preceded by a cleavage in the latter. They

are certainly not identical. The limiting layer is thin at first, becomes gradually thicker, but is never as clearly definable at its edges as are the membranes that follow. It consists of a substance that possesses a different staining capacity from the surrounding cytoplasm and while the cytoplasm is more or less coarsely reticulated or foamy in structure, it on the other hand is apparently structureless or very finely granular. But it is never separable from the protoplasm on either side. The cases of separation figured by Harper are evidently separations between the plasma membranes. Now it is not improbable that with the increased growth and differentiation of the limiting layer, and a pull on the part of the nucleus, that the cleavage is first affected in the part adjacent to the centrosome. It is here that the membranes first begin to form, and it is this part that would be directly affected by a nuclear tension. A continuance of cleavage would be favored by the formation of membranes on the surfaces already separated and much more by the differentiation of the spore plasma which by this time at least is in course of progress.

The membrane covering the epiplasm undergoes no further change except in extent and shape according as the spore changes in this respect. It continues to line the epiplasm until the spores are developed, and is the last of the epiplasmic substance to disappear. The membrane covering the spore plasm likewise continues for a time without other changes than in extent and shape to meet the demands of the growing spore, and the various pressures brought to bear upon it. When the spores are nearly matured, however, the exospore begins to be laid down, and with this process perhaps both plasma membranes are intimately connected.

Subsequent to the formation of the plasma membranes one of the chief matters of interest until the spores are mature, consists in the resumption of a spherical form by the nucleus. This change takes place very soon after the completion of the membrane, though the nucleus may first elongate still farther as shown in figure 32 (pl. 8). The neck of the flask-like nucleus contracts, and the result is to thicken it and draw the centrosome away from the periphery towards the center (pl. 8, fig. 34). In one respect Hydnobolites differs from the forms already described, for as yet the astral rays have not vanished. Indeed, they are demonstrable until the beak is fully withdrawn (pl. 8, fig. 35), although at that time they begin

to fade out. As soon as the centrosome begins its retreat, the rays begin to spread out in all directions.

Whether these rays are precisely the ones that were found extending out from the centrosomes in the spindle stage cannot be affirmed with absolute certainty. But there seems no reason to think that they are any other, nor that they do not include practically all of those rays. This being the case, there is corroborative evidence that the layer of protoplasm that first delimited the spore does not consist of fused astral rays.

Neotiella albocincta (B. & C.) Sacc.

Harper's ('99) description of spore formation in *Lachnea scutellata* is the most detailed account we have of the cytology of the ascus in the Discomycetes. He begins with the uninucleate condition just prior to the first mitosis, and his observations on this stage correspond with those already given by De Bary and Gjurasin. Passing on to the last mitosis, he notes that the daughter nuclei acquire walls before "spore-cutting" is begun. They lie close to the wall of the ascus with their asters directed outward. The base of the nucleus next grows towards the center of the ascus and in this way a beak is formed. The formation of the spores takes place in the manner previously indicated for Erysiphe, so that in Lachnea, too, the spore plasm is "cut" out by a plasma membrane consisting of fused astral rays. He found that there was no aggregation of protoplasm at the time the spores were delimited. He had previously described (Harper, '97) an aggregation in *Peziza vesiculosa* as far back as the four-nucleated and four-spindle stages, but concludes from a re-examination that his previous observations were wrong.

Neotiella albocincta has proved valuable in a study of this kind because of the fact that its nuclei are unusually large, and its protoplasm is free from undesirable substances. Extranuclear bodies are of rare occurrence. The stages in the early development of the ascus, too, are readily followed, but this phase of the subject will receive consideration later on. The material was collected in small quantity near Toronto, Ontario, in the latter part of October, 1902.

Beginning with the mature uninucleated condition (pl. 9, fig. 40) it is noticeable that, unlike most forms, the ascus has not yet attained its maximum size. There is the same differentiation of

protoplasm that Harper noted in Lachnea though the dense portion is not sharply bounded off by concave surfaces, but streams out irregularly into the foamy protoplasm above and below. The nucleus occupies the middle of the dense cytoplasm, though this position is by no means a fixed one. It is perhaps the largest nucleus so far recorded for the Ascomycetes. It possesses a large nucleolus, and well defined and abundant chromatic threads. At this stage, with Flemming's triple, the nucleolus stains a bright red, and the chromatin blue.

The first spindle stage is characterized by a number of interesting features. Throughout karyokinesis the reaction of the chromatin towards the triple stain is changed, for now it dyes a bright red. The spindle is especially clear (pl. 9, fig. 41). It is comparatively broad at the middle and tapers at both ends to terminate in very small centrosomes. From these centrosomes there stream out fine rays which are exceedingly difficult of demonstration. Indeed, in figure 42 (pl. 9) in which the centrosomes lie in the plasma membrane of the ascus, the astral rays appear to be lacking. The long axis of the spindle may lie in any plane from the vertical to the transverse. The nuclear wall degenerates early, and may be gone before the equatorial-plate stage is reached. The nucleolus suffers a very apparent reduction in size during the construction of the spindle. The chromosomes are large, six or seven in number (judging from the number of daughter chromosomes, figure 41), and are horseshoe-shaped. At first the arms of the horseshoe are thick, but as they are pulled back towards the poles of the spindle, they become much more attenuated (pl. 9, fig. 43). During the anaphase stage the centrosomes are no longer to be seen. If present they are obscured by the masses of chromatin. The daughter nuclei are prominent and often contain two nucleoli. But in these as in all resting nuclei belonging to this plant, no centrosomes could be detected.

The details of karyokinesis in *Peziza rutilans*, lately described by Guilliermond (:03a) bear a close resemblance to those I have just described for Neotiella. There are protochromosomes in both, and the chromosomes are U-shaped, especially in the anaphase stage, but twelve in number in *Peziza rutilans*. Guilliermond states that the nuclear wall disappears in the prophase stage, and that neither asters nor centrosomes exist. Because of the absence of astral rays,

an account of the method of spore formation would have been highly desirable.

Though on a smaller scale, the divisions of the second (pl. 9, fig. 44) and the third (pl. 10, fig. 49) sets of nuclei are practically repetitions of the first. It is noticeable with them, too, that the spindles may lie in any plane. The chromosomes, however, in both and especially in the third set are much more slender and more closely massed together. During the last mitosis the protoplasm begins to aggregate about the nuclei.

It is towards the end of this stage that spore delimitation begins. The daughter chromosomes have massed together at the poles of the spindle, and the latter has elongated bringing the eight immature nuclei near the walls of the ascus (pl. 9, fig. 45). The spindles may lie in any plane. Extending out from the poles in some cases can be detected a curved hyaline line, the beginning of the limiting layer similar to that described for Hydnobolites. Walls now soon form about the nuclei which immediately after grow in towards the center of the ascus, in this way acquiring a beaked shape (pl. 9, fig. 46). Their chromatin has passed into a reticular condition, though still massed in the beaked end of the nucleus. Already a nucleolus has made its appearance. The limiting layer of protoplasm advances progressively until completed at the opposite pole, and is considerably thicker than when first seen. At this time the spore plasm is distinctly differentiated.

The succeeding stage (pl. 9, fig. 47) is characterized mainly by an elongation of the beaks, by some growth of both nucleus and spore plasmas, and a continued differentiation of the latter. The plasma membranes then begin to form.

These plasma membranes as in the case of Hydnobolites are two in number: one covers the spore plasma and the other lines the epiplasm in which the spore lies. They are formed, too, on the site of the limiting layer. Their organization begins adjacent to the centrosomes, and, associated with the process of cleavage, continues along the limiting layer until the opposite end of the spore is reached. It is at this stage that surface tensions indicative of a plasma membrane are first apparent. In figure 48 (pl. 9) the membranes are but half formed, but in figure 50 (pl. 10) they are complete. The upper spore in figure 50 (pl. 10) shows an interesting phenomenon that occurs occasionally, namely, the possession of two beaked nuclei.

The spore plasm has in the meantime become very finely reticulated, and the epiplasm is very coarse. Likewise the spore has assumed a regular oblong shape which is retained. The nuclear beak retracts, but in so doing the bulb of the flask is drawn up some distance towards the attached end (pl. 10, fig. 51). The centrosome has disappeared. A period of growth now ensues for both the spore and its nucleus (pl. 10, fig. 52). After the spore has reached about its maximum size the exospore is developed, and when this is finished the epiplasm is practically exhausted.

Sordaria fimicola (Rob.) Ces. & DeNot.

We owe our knowledge of the cytology of the ascus in the Perisporiales to the investigations of Professor Harper ('97) on *Erysiphe communis*. Outside of this order the only member of the Pyrenomycetes to receive attention has been *Cordyceps ophioglossoides*, and this at the hands of Lewton-Brain (:01). Unfortunately Lewton-Brain attempted a cytological investigation on material that was not suitably fixed. He even failed to see the nuclei, evidently mistaking the nucleoli for them. He states that no formation of spores takes place until all nuclear divisions are completed. The nuclei then arrange themselves in eight rows, and the delimitation of these rows and the separation of their nuclei by septa follow. It is in this way that the septate spores originate.

The writer has examined the same form preserved in Flemming's weaker, and finds that the nuclei possess membranes, chromatin, and nucleoli. The only respect in which they deviate from the type is in the possession by the fusion nucleus of small cones. These cones are extranuclear and lie outside the nuclear wall at opposite poles. The nuclear divisions are likewise typical. All the stages in spore formation were not followed, but there is reason to believe that the young spores are uninucleate, and that the multinucleate condition arises by nuclear divisions within the spore.

The Pyrenomycetes are, in general, for various reasons, difficult to manipulate. Of the forms studied none has proved more favorable for examination than *Sordaria fimicola*. The methods employed in growing material have already been described.

The ascus most frequently springs from a curved terminal cell of an ascogenous hypha, much as in the case of *Genea hispidula* (pl.

11, fig. 76). Sometimes, however, the tip is segmented off in the conventional manner, and then the ascus grows out from the penultimate cell. Not all the nuclear phenomena have yet been elucidated, but such as have been, present no new features.

Early in the development of the ascus, extranuclear bodies make their appearance about the "fusion" nucleus. They are in the form of granules or flat masses which lie close against the nuclear wall. They are not scattered about the protoplasm or away from the nucleus as was found to be the case in certain stages in the development of the asci of Hydnobolites. Figures 60 and 61 (pl. 10) represent similar bodies in species of Podospora, in which, however, they are larger than in *Sordaria fimicola*. The number of these bodies is at first small, perhaps not more than one or two, but later on there may be a dozen of them around a single nucleus. Just before the first spindle is formed they disappear and do not again occur. They are probably homologous with Guilliermond's "corpuscules métachromatiques."

There is the same differentiation of protoplasmic contents that we have already observed in *Neotiella albocincta*, and the first nucleus lies within the thick protoplasm. This nucleus, however, does not contain nearly as much chromatin as the corresponding one in Neotiella, though the achromatic network is well developed. The centrosomes throughout are flattened and disc-shaped in the resting nuclei, but smaller in those that are dividing.

The first spindle is prominent, though very slender, is intranuclear, and possesses long, fine astral rays which are demonstrated with some difficulty. Its long axis lies in the long axis of the ascus or very nearly so. In connection with the second set of spindles there are no new features, and the only point to be mentioned is the same extreme lengthening in the anaphase stages that has been noted elsewhere. The resting nuclei at the end of this division attain a fairly large size, and their centrosomes are particularly clear (pl. 10, fig. 53).

During the four-nucleated stage, a differentiation of the thick protoplasm may begin, though the heaping up of the protoplasm about the nuclei becomes much more obvious during the spindle stage that follows. From figure 54 (pl. 10) it will be seen that the protoplasm in the immediate neighborhood of the nuclei is finely reticulated, while farther away vacuoles or coarser reticulations are

evident. This differentiation of spore plasm becomes more and more pronounced from this time on. During the closing stages of the last mitosis the spindle grows out through the ends of the nuclear wall, leaving behind the nucleolus and what are perhaps collapsed remains of the wall. The chromatin is massed against the centrosomes which have come into very close relation with the plasma membrane of the ascus. Just what has caused this elongation and just what the nature of the connection is between centrosomes and plasma membrane are difficult questions to answer. Fine astral rays stream out from the ends of the spindles of the last set and it may be possible that some of these do pass into the plasma membrane and then contract, the contraction resulting in the elongation of the spindle and the drawing of the centrosomes to the wall. This would explain the depressions in the plasma membrane adjacent to the centrosomes and their connection with the former (pl. 10, fig. 55).

The explanation offered by Harper ('99) of similar depressions in Lachnea was that they were caused by the astral rays pulling out of the membrane preparatory to "cutting" out the spore mass. Obviously such an explanation assumes an exercise of considerable force by the rays, for unless the pull be straight in line with the spindle the rays are at a mechanical disadvantage. Moreover, unless the pull be in line with the spindle (which assumes that the middle rays must be very short, which is contrary to fact) the center of depression would not be adjacent to the centrosomes.

The limiting layer of protoplasm that separates the spore plasm of a future spore from the epiplasm begins to form during the final anaphase stages of the fourth spindle (pl. 10, fig. 55). It extends out from the centrosome following for a way closely along the plasma membrane that lines the wall of the ascus. The layer is progressively formed until completed at the pole opposite the centrosome. Primarily very thin, it eventually thickens and becomes more conspicuous. Meanwhile the walls have formed about the daughter nuclei and this is immediately followed by a growth of the nuclei resulting in the flask shape or beaked form (pl. 10, fig. 56).

As soon as the spore masses are delimited, the plasma membranes are developed. They are formed in the plane of the limiting layer, and the phenomena of their production are the same as described for Hydnobolites and Neotiella.

The young spores when first delimited, are much compressed in shape, but they soon acquire the oblong shape indicated in figure 57 (pl. 10). In figure 57 the plasma membrane is completed and the nuclear beak has reached its maximum length. This beak has become more tenuous than formerly and the chromatin has been distributed.

The centrosome soon breaks from the plasma membrane and the beak is retracted. This retraction is preceded by a contraction which results in its thickening and in drawing the venter of the flask nearer the end of the spore.

This re-formation of the nucleus is directly followed by its division. The division is karyokinetic. The spindle is intranuclear and there are asters. In the anaphase stage it elongates beyond the limits of the nuclear wall which soon after disappears (pl. 10, fig. 58). When completed, the daughter nuclei resemble the mother nucleus in all respects except in size (pl. 10, fig. 59). The exospore has not yet been laid down, though its appearance is now not long delayed.

Septate and Multinucleate Spores.

Multinucleate spores are generally septate. *Sordaria fimicola*, as we have seen, affords an example of a departure from this rule. The spores of *Discina venosa* are several-nucleated and yet not septate, while those of a Thielavia found by Professor Thaxter at New Haven, growing parasitically on Isaria, regularly contain four nuclei. When first formed, all possess but a single nucleus, the increased number arising by subsequent divisions proved in *Sordaria fimicola* to be karyokinetic.

Septate spores are likewise uninucleate at their origin. This has been shown to be the case in various forms examined by the writer, such as *Massaria vomitoria*, *Massaria platani*, *Geoglossum ophioglossoides* and *Geoglossum hirsutum*, *Leptoglossum* sp., and *Leptoglossum luteum*. The spores are nearly spherical when delimited, but after the development of the plasma membrane they begin to elongate. In course of this growth in length the nuclei divide and septa are usually formed after each division, thereby separating the daughter nuclei from one another. The nuclei seem to be intimately connected with the construction of septa, for septa are formed in

their immediate neighborhood only. In *Cordyceps ophioglossoides* young spores were observed that contained but a single nucleus and in all probability the subsequent steps in development do not materially differ from those occurring in a Massaria or a Geoglossum.

The spores of several of the Podosporas present a curious case of the formation of a septum without a previous division of the nucleus. This practically amounts to cutting off from the spore a part that persists as an appendage or tail and maturing the part only in which the nucleus lies. Such tailed spores occur in *Podospora setosa*, *P. anserina*, *P. fimiseda*, *P. curvula*, etc. *Podospora curvula* illustrates very well the steps in the development of such spores. The preliminary stages are similar to those that take place in *Sordaria fimicola*. The spore plasm is also delimited as in Sordaria, though early aggregation of the protoplasm is not so readily observable. The young spores are at first compressed (compare with figure 56, plate 10) but rapidly change in form so that the nucleus appears to be attached to the end and not to the side of the membrane. The shape of the spore at this time is cylindrical or rod-like. This is followed by an enlargement of the upper end in which the nucleus is to be found. It next moves down to the entrance of the small end (pl. 10, fig. 62), for it has grown too large to go any farther. This step is preparatory to the cutting off of the tail.

A septum is evidently formed through the activity of the nucleus. That the latter is more active than usual is shown by the fact that the cytoplasm in its immediate neighborhood gives a staining reaction with Flemming's triple different from that in the rest of the cytoplasm (pl. 10, fig. 62). In any case a wall is laid down at this time and just below the position occupied by the nucleus. The wall having been formed the nucleus passes once more to the center of the upper part (pl. 10, fig. 63). The tail develops no further, and gradually loses its protoplasm. Whether or not the septum partakes of the character of a plasma membrane may not be decided with certainty. But the exospore is developed in connection with this part as with the rest of the wall surrounding the nucleated portion. That it is developed but very slightly on the tail, which grows but little more, is proof that the nucleus to some extent at least controls the laying down of the exospore.

Origin of the Ascus.

According to the researches of Dangeard ('94) and Harper (:00) the ascus originates from the cell next to the terminal one. After an examination of thirty-six species from which it is possible to determine this matter, it has been found that such is invariably the case in but eleven of them.

Maire (:03) and Guilliermond (:03a) have recently reported deviations from the conventional type in *Aleuria cerea* (?), and *Galactinia succosa*. In the former the ascus arises from a penultimate cell in which there are two nuclei, but the terminal cell likewise contains two nuclei. In *Galactinia succosa* the end of the hypha is not hooked, the last two or three cells enclose two nuclei each, and the ascus springs from the terminal cell.

The most frequent deviation from what has been taken as the conventional type is that represented in figure 74 (pl. 11) for *Genea hispidula*. In this case the ascus grows out from a curved terminal cell. It is quite probable that the only departure from the type is the lack of the cross wall that cuts off a uninucleated cell at the tip of the hypha. Other forms that resemble *Genea hispidula* in this respect are *Podospora anserina*, *P. setosa*, *Sordaria fimicola*, *S. humana*, *Geoglossum ophioglossoides*, *G. hirsutum*, *Geoglossum* sp., *Verpa conica*, *Gyromitra sphaerospora*, *Leptoglossum luteum*, *Leptoglossum* sp., *Mitrula phalloides*, *Leotia lubrica*, *L. chlorocephala*, *Phyllachora graminis*, and *Discina venosa*. In some of these the missing partition is found to be present exceptionally.

Of all the forms examined, *Verpa bohemica* exhibits the greatest variability. It has been hitherto stated that asci spring from the penultimate cell and that the terminal one develops no further. Both of these statements may be incorrect as far as *Verpa bohemica* is concerned. Thus, asci sometimes occur as represented in figure 79 (pl. 11) as outgrowths of a terminal cell. In the case figured there is a second outgrowth which is perhaps of later origin than the ascus. Again, the ascus may be found to grow out from the second, third, or even fourth cell from the end (pl. 11, figs. 71, 72, 75, 77). It remains to be determined yet whether the terminal cell underwent divisions after the budding out of the ascus, or whether the ascus may grow out of the third or fourth cell as it sometimes does from either the first or the second. In *Anixia*

spadicea (pl. 11, fig 80) and *Urnula craterium*, it looks as if the ascus might spring from any cell whatever. The Anixia was obtained from a culture given me by Professor Thaxter.

A number of forms were found to follow very closely the type described by Harper and Dangeard. These were *Peziza* sp., *Neotiella albocincta*, *Morchella esculenta*, *M. conica*, *Helvella atra*, *H. lacunosa*, *H. elastica*, *Acetabula* sp., *Pseudoplectania* sp. In Hydnobolites and Elaphomyces the ascus usually grows out from the second cell, though occasionally the end septum is lacking.

The cytological phenomena in connection with the origin of the ascus are quite readily worked out in the Helvellas, Neotiella, and Peziza. Neotiella was found an especially favorable form because of the size of its nuclei and the absence of extranuclear bodies.

The earliest stage of all, however, was observed in *Peziza* sp., in which the hooked end of an ascogenous hypha was found with a nucleus in each arm of the hook. These nuclei were also observed in a condition of mitosis (pl. 11, fig. 64). Of the four daughter nuclei the proximal one is soon shut off by a septum (pl. 11, fig. 65). This was the first stage found in Neotiella. A second septum was then formed cutting off the distal nucleus (pl. 11, fig. 66) and leaving the two middle nuclei in a penultimate cell. It is from this cell that the ascus grows out. The two nuclei fuse either before or after they enter the young ascus (pl. 11, fig. 69). In *Urnula craterium* the fusion is always effected in the ascus and not until it has attained a considerable length.

This fusion apparently consists in the disappearance of the parts of the nuclear walls in contact, and the flowing together of the chromatin and the nucleoli. The "fusion" nucleus rapidly rounds up unless the fusion has taken place in the ascus. When the "fusion" nucleus lies in the ascus it is always elongated because its diameter is greater than that of the ascus (pl. 11, fig. 68).

The nuclei of the first and third cells usually disappear very soon after the ascus has begun its growth, and the same is true of the protoplasm in the cells in which they lie. It is too much to say, however, that such is the constant fate of both, and especially of the proximal one. The origin of the four nuclei found in the hook cannot be stated with absolute certainty. There is reason to believe that they may be products of a single nucleus in some cases. Thus it is a matter of observation that an ascus-bearing hook may be

developed from a cell removed but one from an ascus and this cell may contain a single nucleus (pl. 11, fig. 66).

General Considerations.

The problem of the origin of the Ascomycetes must be attacked along two main lines, namely, a determination of the homologies of the ascus, and an appreciation of the phenomena associated with the sexuality of the group. These, it is to be pointed out, are separate questions, although it is also true that a final solution can be effected only after a consideration of both. The present research has only to do with the question of the homologies of the ascus.

Asci are now generally regarded as asexually produced spore sacs on hyphae which are outgrowths of a fertilized organ. Most botanists agree on the view that the Ascomycetes have not lost the sexual method of reproduction, and that in some of them at least there are functional sexual organs. What was a conviction of De Bary's has been proved by the researches of Harper (:00) and Thaxter ('96) to be a reality. The sexual organs are borne on a mycelium that follows the germination of the ascospores, and from the fertilized oogonia or ascogonia there grow out the ascogenous hyphae, and it is from the cells of the latter that the asci arise. These observations may, I think, be assumed without further remark to be correct. The next question that arises, and on which there is not such unanimity, is in regard to the ancestral homologue of the ascus.

On this subject four suggestions have been offered: (1) that the ascus is a descendant of the sporangium of the higher Mucorineae through the Hemiasci, a theory that was propounded and stoutly maintained by Brefeld; (2) that the ascus is a derivative of the sporangium (or zoosporangium) of the Oomycetes; (3) that it is a new feature without a homologue outside the Ascomycetes; and (4) that it is a modification of the carpospore of the Florideae.

The phenomena of the early stages in the development of the asci unfortunately do not throw much light on this matter, unless, indeed, to confirm the view that they are coenogenetic organs. The fusion of nuclei within the young asci, the phenomenon to which I especially refer, is a puzzling feature, one that is as yet

unknown to occur in the history of any Phycomycetous sporangium or Floridean carpospore. Dangeard ('94), who first made its discovery, considers it a sexual act, but this conclusion scarcely seems plausible because the following facts appear to have been satisfactorily demonstrated in several instances: (1) there has already been a fusion of sexual elements in the ontogeny of the individual, (2) the fusing nuclei in the ascus are division products of nuclei belonging to the same cell, and perhaps in some cases even daughters of sister nuclei, and (3) they are vegetatively active before fusion, as is the single nucleus after fusion. The phenomenon is probably vegetative rather than sexual, but its nature and significance will not be fully understood until further research reveals whether or not it is an acquired feature.

Fortunately more exact comparisons can be instituted in dealing with the later events in the life of the ascus. Hence the homologies of the ascus will at present be dealt with mainly from the standpoint of the phenomena of spore formation, and in the light of these phenomena each of the foregoing suggestions will be briefly considered in turn.

Brefeld was the champion of the first suggestion for he regarded the sporangium of Mortierella or a closely related form as the ancestor of the ascus, but it is doubtful if his position is tenable on cytological grounds, though the cytology of this particular genus has not been described, yet owing to the careful work of Harper ('99) and recently of Swingle (:03) we know quite fully the cytological details of spore production in such closely allied genera as Pilobolus, Rhizopus, Sporodinia, and Phycomyces. In all of these forms, spore formation is initiated by a segregation of the spore plasm into a cell, the sporangium. The next step consists of a progressive cleavage of the spore plasm into irregular multinucleate masses, the cleavage beginning at the surface of a plasma or a vacuolar membrane. There is no residue of epiplasm. These masses may round themselves up into spores at once as in Sporodinia, or they may undergo further cleavage. In the latter case the later cleavage furrows do not curve, intersect, and branch in the same irregular way as do the earlier, but they seem to bear a more definite relation to the nuclei and in Pilobolus are first marked out by a development of hyaline zones. Harper is therefore apparently justified in concluding that since the method of sporogenesis in these sporangia dif-

fers in so many important respects from what has been described for the asci, it is difficult to see how the asci could possibly have been derived from them.

Nor has a study of Brefeld's so called intermediate forms revealed a connecting link between the Zygomycetes and the Ascomycetes. A number of the Hemiasci have been examined from this point of view by Popta, Holtermann, and Juel, and though some points have not been cleared up, yet the conclusion is fairly safe that their sporangia do not occupy the intermediate position that has been claimed for them.

Holtermann ('98) has described the method of spore formation in a Hemiascous form called by him *Oscarbrefeldia pellucida*. He says of this that in the young ascus the granular protoplasm lines the wall, while the center is occupied by hyaline cell sap. Soon a plate of protoplasm forms across the ascus dividing the central cavity into two parts. In a similar manner the cavity is finally divided by a succession of protoplasmic plates into as many as thirty-two hollow spaces, the interior of the future spores. These small cavities then round themselves up, a cuticularized layer is formed about them, and the spores are completed. There is a residue of epiplasm. He confesses that "Ich habe mich hier auf eine einzige Art [the culture method] beschränkt"; but gratuitously adds "aber nach den vorläufigen Untersuchungen hege ich keinen Zweifel, dass die Bildung and Differenzierung der Sporen bei den anderen Ascomyceten nicht wesentlich abweicht von der des oben beschriebenen Falles." The unfortunate part of his investigations was his failure to recognize the existence of nuclei in fungi. "Denn es würde sich dann sofort herausgestellt haben, dass das, was bis jetzt für Zellkern bei den Pilzen gehalten wurde, theils Vacuolen, theils Protoplasmaansammlungen, theils auch Protoplasmakörnchen sind."

Observations on three of the Hemiasci, *Ascoidea rubescens*, *Protomyces macrosporus*, and *P. bellidis* have been recorded by Popta ('99). In *Ascoidea rubescens* the spores are formed by the protoplasm becoming more densely aggregated about the nuclei, followed by a development in an undiscovered manner of limiting walls. There is an epiplasm. In each of the other forms the protoplasm arranges itself in a parietal layer leaving a vacuole in the center. The division planes in *P. bellidis* are radially arranged, suggestive

of the method of spore delimitation in Saprolegnia. While there is but one layer of spores in this species, there are three in *P. macrosporus*, and in both there is no epiplasm. It is to be regretted that Popta examined living material only.

And finally Juel (:02) has described the process of sporogenesis in *Taphridium algeriense*. According to his description the protoplasm is differentiated into a denser portion that lies at the periphery and in which the nuclei are arranged in a single layer, and a vacuolated portion that fills the rest of the sporangium. Uninucleated spores are now formed from the dense protoplasm, but Juel could not determine how delimitation was effected.

The details of spore formation in the Hemiasci given us by these investigators are apparently too meager to enable us to come to a final conclusion, but it seems quite unlikely from such as are known that the "sporangia" of the Hemiasci are intermediate between Mortierella-like sporangia and asci. It is evident that the latter are not only not directly connected, but also that they are not linked to one another by means of such forms as Protomyces and Taphridium. Nevertheless I cannot agree with Harper ('99) that "the total dissimilarity of the process of cleavage in the sporangia described [Pilobolus and Sporodinia] and the ascus, makes it necessary to look for the ancestors of the Ascomycetes elsewhere than in the lower Fungi," for it is to be noted that the forms he investigated were of a highly specialized type. If the ancestral homologue of the ascus is a sporangium at all, it is more likely to be found among more primitive sporangia than Harper described. This brings us to the second suggestion, namely, that the ascus is a derivative of an Oomycetous zoosporangium.

Spore formation in the lower Phycomycetes has received some attention at the hands of Hartog ('88), Rothert, Humphrey ('93) and more recently Davis (:03). In their descriptions of the cytology of the zoosporangia of the Saprolegniaceae they agree on the general features. The central part of the sporangium becomes vacuolar, the vacuoles flow together and form a large cavity filled with sap. The protoplasm thus occupies a peripheral position. Radial clefts then start from the vacuolar membrane cutting the cylinder of protoplasm into the spore origins, which contain a single nucleus each, and which without further division are transformed into zoospores.

Leaving aside for a moment their relative ontogenetic values it

is to be enquired if the sporogenesis of such a sporangium could not be homologized with that of the ascus, or in other words if the ascus might not find its ancestor in a Saprolegniineous zoosporangium. If so, then we may with more reason look for the ancestors of the Ascomycetes among the lower fungi. There are, of course, marked differences in the sporogenesis of zoosporangium and ascus, but that is to be expected, — they exist between even the sporangia of Saprolegnia and Mucor, which are with little doubt rather closely allied, — for if the Ascomycetes be connected phylogenetically with the Saprolegniineae they are removed at a great distance as is shown by the characters of their vegetative bodies and organs of reproduction, differences which, it is needless to say, have arisen through the acquirement of very different habits. But these differences may not be found to be irreconcilable with a theory that connects the two phylogenetically. For instance, a most striking difference is the fact that the sporangium is multinucleate from the beginning while the ascus starts in a binucleate condition; but this might be accounted for without difficulty if it is granted that a septate thallus, the cells of which are one- to few-nucleated, may arise from a coenocytic thallus. Likewise it will be found that other differences are not so formidable as they appear at first sight, and that taken with the similarities they may not be such as to debar connecting the one with the other.

In the preparations leading to the formation of the spores there are two phenomena which in general are the same in both the zoosporangium and the ascus, and which may not be without significance: (1) the differentiation of the protoplasm into dense and vacuolated portions, (2) the migration of the nuclei to a peripheral position in the dense protoplasm. In regard to the differentiation of the protoplasm, it is worthy of note in this connection that in the ascus, vacuoles frequently occur in a more or less central position directly following the last nuclear division. Harper ('99) noted these vacuoles in Lachnea, but ascribed them to the escape of nuclear sap in the anaphase stages of the last mitosis. This explanation does not seem adequate, however, to account in many cases for the size, number, and position of all of them, even if it be granted that the escape of nuclear sap might be responsible for some.

From this point on, the processes are apparently much more

unlike, and the following differences have been insisted upon by certain botanists as being incompatible with any view that homologizes ascus and sporangium: (1) that in the sporangium the nuclei are perhaps not at all functional in the delimitation of the spores, while in the ascus they are the direct agents; (2) that the process of spore delimitation in the first case is an act of cleavage (previously or not at all marked out by hyaline areas), while in the latter it is a literal cutting out of the spore plasm by a plasmatic membrane; (3) that the plasma membranes of the sporangiospores are extensions of previously existing plasma membranes, while those of the ascospores are composed of fused astral rays; and (4) that there is an epiplasm in the ascus, but none in the sporangium, and that this is because of two fundamentally unlike methods of spore delimitation.

There is, I am inclined to think, some question as to the validity of the first of these contentions in regard to the sporangium. Thus, as far as Saprolegnia is concerned, nuclear control in spore formation seems almost a certainty, for the spores that are formed are constantly uninucleated and never enucleated, and the nuclei are practically the centers of the cleavage areas. And even in the Zygomycetes it is difficult to conceive of control being entirely transferred to the cytoplasm, for, in the forms that have been investigated, it is notable that nuclei are never absent from the protoplasmic masses resulting from the cleavages. Incidentally it may be observed that if spore formation in the Zygomycetes is due to the activity of the cytoplasm, but in the Oomycetes to the activity of the nuclei, then it would appear that the value of the cytology of spore formation as a factor in deciding phylogenetic problems between fairly widely separated groups is rather questionable.

Nuclear control in the Ascomycetes is undoubted. Indeed, certain phenomena demand comment. Thus even the shape of the nuclei changes throughout the process, a feature that seems unique. Timberlake (:02), however, has observed somewhat similarly shaped nuclei in some cases in Hydrodictyon, and his observation was that the pointed end lay near the newly formed plasma membranes and that the occurrence was only noted when cleavage followed closely on nuclear division. In explaining this phenomenon it must be borne in mind that spore-forming in the Ascomycetes is precocious, that the spores are being delimited and the spore plasma differenti-

ated concurrently with the growth of the nuclei, and frequently with their reconstruction, and that these changes are taking place in the same direction as that in which the nuclei are elongated. The question of the part played by the astral rays, however, is a more serious one. That they certainly do not form the limiting membrane but are enclosed within the spore is maintained by the observations recorded in this paper. But this does not entirely dispose of them, for it may be suggested that they serve to direct the delimitation of the spore, especially the laying down of the limiting layer of protoplasm (though not forming a part of it) which marks out the cleavages to follow or as Berlese ('99) thought, of the plasma membrane itself. If they are visible expressions of nuclear forces, that is possible, though rather indicative of cytoplasmic activity under nuclear control in the region in which they lie than of an activity or force within themselves. The variability of their appearance leaves it open to question that they are at all essential to the process or take any share in it. In Hydnobolites they are pronounced; in *Neotiella albocincta* they are not abundant, and are very tenuous and difficult of demonstration, and Guilliermond (:03a) claims that in *Peziza rutilans* they are entirely absent. Indeed, the function of astral rays in the ascus remains the same debated question as in other places in which they occur.

As to the second and third objections, namely, in regard to the nature of the delimitation of the spores, and of their plasma membranes, my observations indicate that in both zoosporangium and ascus the process of delimitation is practically the same, — a cleavage, — and that the plasma membranes are the same, and not in the one a fusion of astral rays. The point from which cleavage starts is a secondary matter. Within the Phycomycetes themselves there is great variability, the cleavages beginning from inner or outer plasma membranes or even from vacuoles. Whether or not the plasma membranes about the spores are entirely formed *de novo* in one case and not in the other, seems of little account, granted that they are the same and formed in essentially the same way.

The last objection has to do with epiplasm, its absence in the sporangium and its presence in the ascus. In the former the plasma membranes on either side of a cleft enclose a young spore, while in the latter but one of them performs that function, the other lining a cavity in the non-nucleated epiplasm. This epiplasm has been

looked upon as a natural and a necessary result of a *new* method of spore "cutting," and that it could not have arisen in the zoosporangium. That the *new* method referred to occurs in the ascus has not been borne out by my observations and that epiplasm might not have arisen in a zoosporangium is at least debatable. Granted nuclear control in sporogenesis, and a tendency towards a reduction in the number of spores without a corresponding and synchronous decrease in the protoplasm (a common feature in many Ascomycetes), and add to this, if need be, the acquirement of a precocious habit of spore-forming (especially if this means that the young spores depend to a large extent upon the contents of the spore sac, as is the case in asci) then epiplasm might very naturally be expected to follow in the zoosporangium, and without a change in the method of spore delimitation.

On the whole it does not appear incompatible with the facts to suppose that the homology of a Saprolegniineous zoosporangium with an ascus is at least a possibility, if, of course, there is no ontogenetical disqualification. As to that, if the Ascomycetes have sprung from the Oomycetes, then the regular alternation in the production of sexual and asexual organs exhibited by them has probably come about by the production, in certain transitional Oomycetes, of sexual organs only on the mycelia growing from the zoospores, their zoosporangia being suppressed or transformed into conidia, and the production of zoosporangia only by the mycelia growing from fertilized eggs. The latter zoosporangia have become asci.

It should be stated here that Juel (: **02a**) and Barker (: **03**) have recently expressed the view that the ancestor of the ascus is an Oomycetous zoosporangium. They reach their results, however, by a method that should be used only with great caution. They ground their conclusion on an analogy between spore-forming in the ascus and the oogenesis of the Oomycetes. The *raison d'être* of such an argument is based upon the theory that oogonia and antheridia are derivatives of algal gametangia, and that in the lower algae the gametangia are indistinguishable from and probably homologous with zoosporangia.

For the last two suggestions concerning the origin of the ascus there is little more to be said on the basis of the phenomena of sporogenesis. If the ascus could have been developed from the

Saprolegniineous zoosporangium, then it seems unnecessary to regard it as a new feature. As to its origin from a carpospore there are few known facts on which to base a conclusion, and such as are known are to the effect that the carpospores are uninucleate from the first, and continue to be so to the end.

Of the four suggestions offered, the facts of spore formation that have been adduced up to the present, seem, in the opinion of the writer, to favor the one that homologizes the ascus with the Oomycetous zoosporangium. If established, it is a strong argument in support of the theory that the Ascomycetes have been derived from the Oomycetes. Such a conclusion, however, can scarcely be considered as final, for as was indicated in the opening paragraph of this section, the phenomena of sexuality are equally important in determining the origin of the group, and deserve equal consideration. It is outside the purpose of the present paper to discuss that side of the subject, though it may be added that De Bary on the basis of sexuality arrived at the conclusion that there is a probability of the phylogenetic relationship of the Ascomycetes with some such Phycomycetous group as the Peronosporineae or Saprolegniineae.

Summary.

1. The asci bud out from the penultimate cells of the ascogenous hyphae in some forms, in others from the terminal cells, and in a few species apparently from any cell.

2. In every case that was definitely determined, the uninucleated stage is preceded by a fusion of two nuclei within the ascus. The conjugating elements, though not sisters, may sometimes be the daughters of sister nuclei.

3. The age and development of the asci at the time of fusion vary considerably in different species, and to some extent, though within narrower limits, in the same plant.

4. Extranuclear bodies or granules, evidently of nutritive matter, the staining reactions of which are very similar to those of the nucleolus, are formed in the young asci in the neighborhood of the nuclei, and probably through their activity. They disappear before the spores are matured and in many forms during the first spindle stage. Similar bodies frequently occur in the ripe spores.

5. The spindles are of intranuclear origin, but the centrosomes and asters with which they are typically associated are of extranuclear origin. The wall of the nucleus usually persists until a late anaphase stage, though exceptionally as in *Neotiella albocincta* it disappears before the equatorial-plate stage is passed.

6. The chromosomes vary for different species from four to eight in number. In Neotiella they are comparatively large and U-shaped.

7. Directly following the last mitosis in the ascus, and before the daughter nuclei pass into a resting condition, the spores are delimited and a plasma membrane is organized about them. The phenomena characteristic of this period are as follows: (1) an elongation of the spindle fibers bringing the daughter nuclei to the periphery of the mass of dense protoplasm in which they lie, and their centrosomes into close relations with the enveloping plasma membranes; (2) the delimitation of the spore plasm about each nucleus by the differentiation of a limiting layer of hyaline or finely granular protoplasm that begins adjacent to the centrosome and continues progressively until completed at the opposite pole; (3) the formation of a nuclear wall, the time of the appearance of which is variable for different species and bears no relation to the delimitation of the spore plasm; (4) the elongation of the nucleus after it has acquired a wall, resulting in a pear or beaked form with the centrosome at the end of the beak; (5) the organization of a plasma membrane about the spore plasm and another opposed to it lining the cavity in the epiplasm. These are formed on the site of the limiting layer and are probably preceded by a cleavage in the latter. The cleavage and organization of the membranes begin at the centrosome end of the spore and progress continuously to the opposite pole. (6) Retraction of the nuclear beak then follows and the nucleus assumes its regular spherical shape. Occasionally the centrosome, lying outside the nuclear wall but close against it, may be demonstrable for a short time after this re-formation. Very rarely, as in Hydnobolites, the astral rays persist up to this stage.

8. There is no evidence in the species studied that the astral rays fuse to form a membrane which cuts out the spore plasm and becomes the plasma membrane of the spore. They appear never to fuse, as is stated by Harper to be the case in Erisyphe and Lachnea, and the plasma membranes about the spores have quite a different origin.

9. After a period of growth and storage of reserve matter, an exospore is formed between the two opposed plasma membranes.

10. In the meantime the following changes may take place in the spores, according to the species to which they belong: (1) karyokinetic division of their nuclei without the formation of septa; (2) nuclear division followed by a corresponding septation; (3) the cutting off of an enucleated part of each spore, as in Podospora, by a septum, the organization of which is due to the direct action of the nucleus on the cytoplasm in its neighborhood.

11. The evidence points to the conclusion that while the ascus has probably not been derived from the sporangium of the Mucorineae, the phenomena of spore formation are not incompatible with the view that homologizes the ascus with the zoosporangium, nor with the view that the Ascomycetes have originated from some such Phycomycetous group as the Peronosporineae or Saprolegniineae, an affinity first suggested by De Bary on the basis of sexuality.

The investigations recorded in this paper were begun in the Laboratories of cryptogamic botany at Harvard university under the direction of Prof. Roland Thaxter, to whom I am under deep obligations for material and advice. My best thanks are also due Prof. W. G. Farlow and Dr. E. J. Durand for assistance in determination of species, Prof. E. C. Jeffrey for specimens of Tuber and Balsamia, and Professors C. B. Davenport and D. S. Johnson for facilities afforded in collecting material at the Biological station of the Brooklyn institute of arts and sciences at Cold Spring Harbor, L. I.

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EXPLANATION OF PLATES.

All drawings were made with the aid of a camera lucida. Fig. 69–79 are from cover-glass preparations, the rest from sections.

PLATE 7.

Fig. 1–16, *Hydnobolites* sp.

Fig. 1. Young uninucleated ascus. Differentiation of the contents into dense and vacuolated portions has already taken place. Very small extranuclear bodies lie just outside the nuclear wall.

Fig. 2. Oblique section of an older ascus. The dense protoplasm has become somewhat vacuolated. There are three large extranuclear bodies shown.

Fig. 3. Transverse section of upper part of a still older ascus. There are coarse fibrillar radiations out from the nucleus. The nucleus is surrounded by several small extranuclear bodies.

Fig. 4. Longitudinal section of a more advanced stage than in figure 3. Protoplasm finely reticular and delicately radiate about the nucleus. Extranuclear bodies scattered.

Fig. 5. Longitudinal section at time first aster appears. Extranuclear bodies occur at this stage near the periphery only.

Fig. 6. Equatorial-plate stage of first spindle.

Fig. 7. Same nucleus with spindle as in figure 6.

Fig. 8. First mitosis. Daughter chromosomes are formed.

Fig. 9. Early anaphase stage of first mitosis.

Fig. 10. Spindle elongating in anaphase stage of first mitosis. Chromosomes have reached the poles.

Fig. 11. First mitosis. Nuclear wall has disappeared. Protoplasm more coarsely reticulated except in the immediate neighborhood of the nucleus.

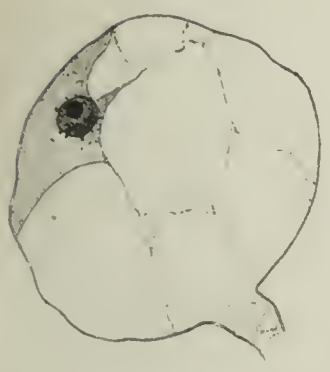
Fig. 12. Same spindle as in figure 11.

Fig. 13. End of first mitosis, showing extreme elongation of spindle and the vanishing nucleolus.

Fig. 14. One of the two daughter nuclei following first mitosis in resting condition. Single centrosome. The dense protoplasm is now uniformly and rather coarsely reticulated.

Fig. 15. Somewhat later stage than in figure 14. Protoplasm surrounding the nuclei begins to become finely reticulated and radiate. The fusion of vacuoles below is practically complete thus providing the dense protoplasm with a continuous plasma membrane.

Fig. 16. Two-spindle stage in longitudinal section of ascus.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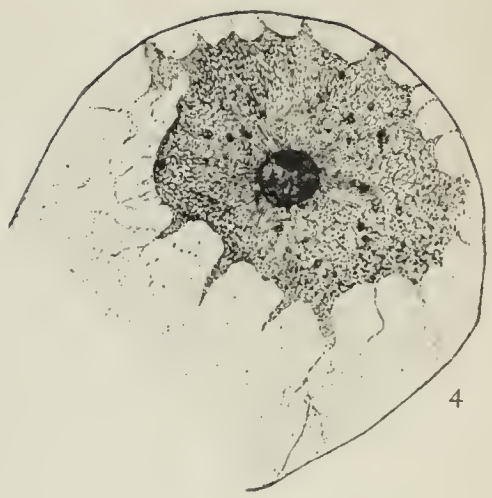
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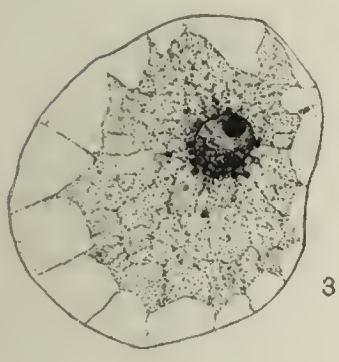
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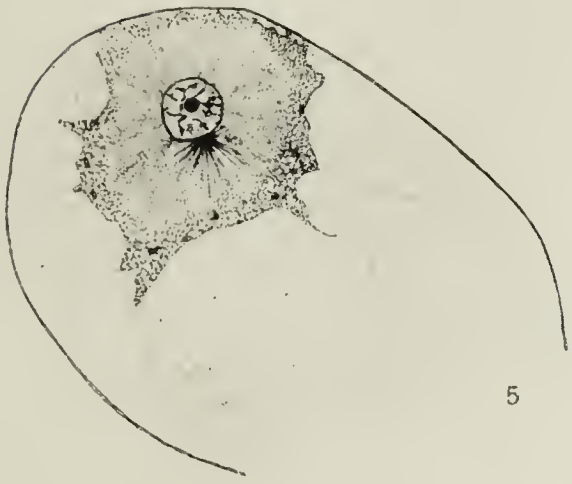
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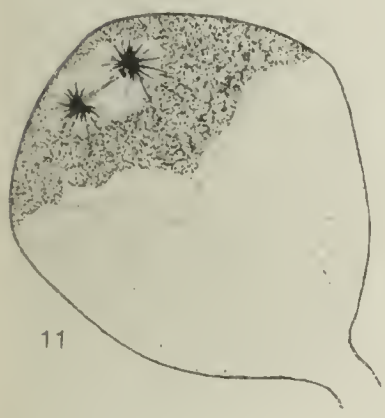
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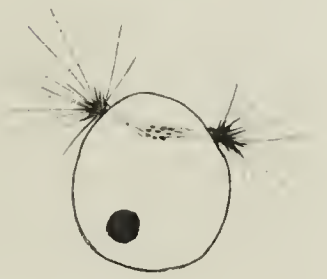
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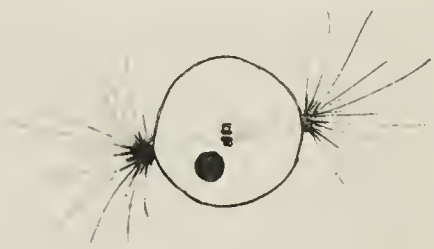
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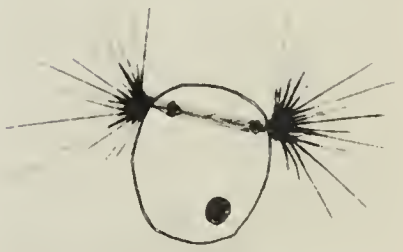
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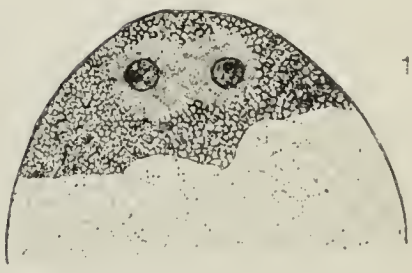
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PLATE 8.

Fig. 17–39, *Hydnobolites* sp.

Fig. 17. One of the spindles in figure 16. Late anaphase stage. Collapsed remains of the old nuclear wall still persists.

Fig. 18. Three of the four daughter nuclei in resting condition following second mitosis. Centrosomes are shown with two of them.

Fig. 19. Three of the four spindles of last mitosis.

Fig. 20. Spindle slightly younger than in figure 19, showing a mantle.

Fig. 21. Transverse section of top of ascus at end of last mitosis showing a polar view of five daughter nuclei.

Fig. 22. Intranuclear view of pole of the spindle of about the same age as in figure 19.

Fig. 23. Vertical section of nucleus of about the same age as in figure 21 or a little older. Spore plasm becoming differentiated in neighborhood of nucleus and the limiting layer beginning to form. Uppermost line represents wall of ascus.

Fig. 24. Older stage than in figure 23. Limiting layer not yet complete and nuclear wall hardly evident; dense protoplasm quite vacuolated.

Fig. 25. Polar view of about same age as in figure 23 or 24.

Fig. 26. Considerably later stage than in figure 24. Part of wall of ascus is drawn. The cylindrical nucleus is very obvious. The limiting layer is completed and already the plasma membranes are half completed.

Fig. 27. Later stage than in figure 26.

Fig. 28. Same age as in figure 27.

Fig. 29. The plasma membranes are nearly completed. They are somewhat separated from one another at upper pole.

Fig. 30. Plasma membranes completed.

Fig. 31. Same as in figure 30. Spore beginning to round out.

Fig. 32. As in figure 31 the centrosome is distinct. Both nucleus and spore show a lengthening.

Fig. 33. A polar view of about the same age as in figure 29 or 30. The astral rays have never exhibited a tendency to fuse laterally. The plasma membranes are separated.

Fig. 34. Retraction of nuclear beak under way.

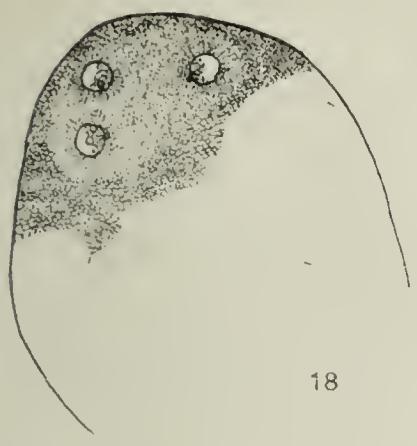
Fig. 35. Nuclear beak entirely retracted.

Fig. 36. Astral rays have disappeared. Centrosome is only occasionally demonstrable after beak has been withdrawn. Plasma membranes of spore and epiplasm are considerably separated at one side of spore.

Fig. 37. Nucleus of spore in a resting condition. Directly after this the spore begins to elongate.

Fig. 38. Longitudinal section of ascus at about the stage represented in figure 29 showing relation of young spores to plasma membrane surrounding dense protoplasm.

Fig. 39. Transverse section of upper part of ascus at same age and for same purpose as in figure 38.



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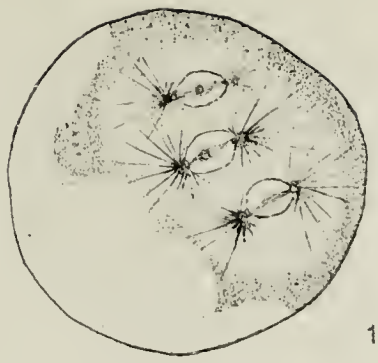

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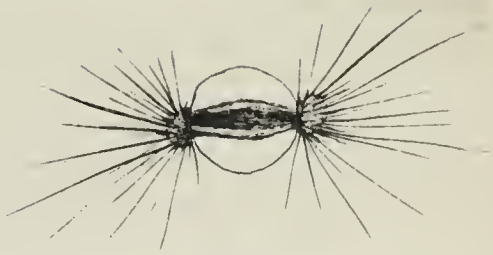

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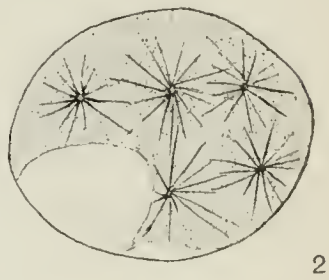

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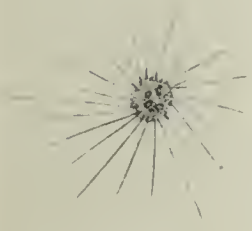

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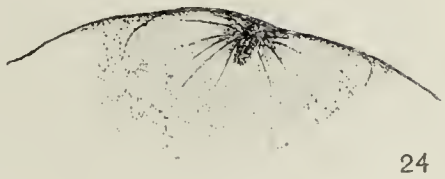

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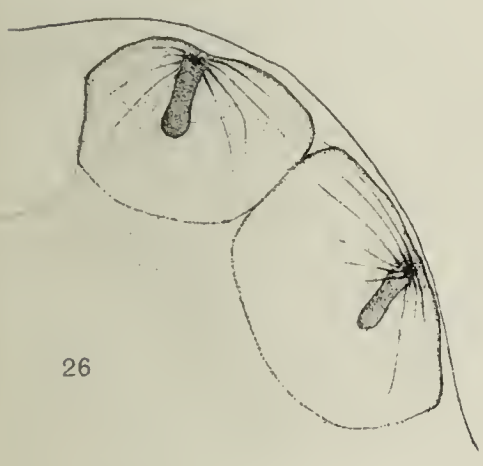

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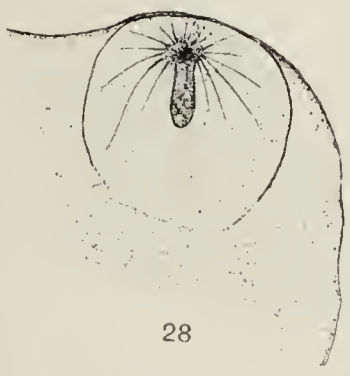

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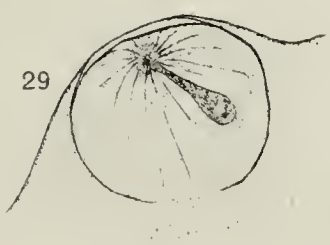

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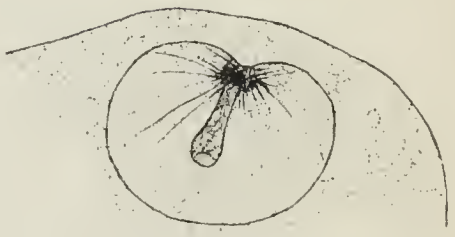

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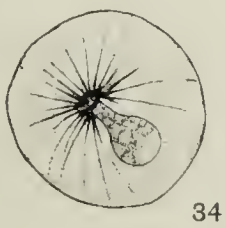

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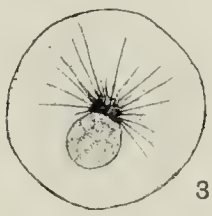

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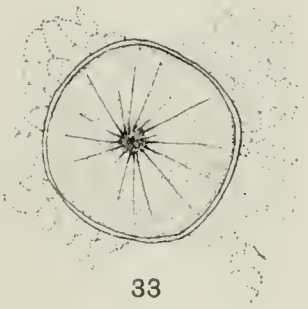

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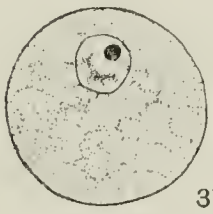

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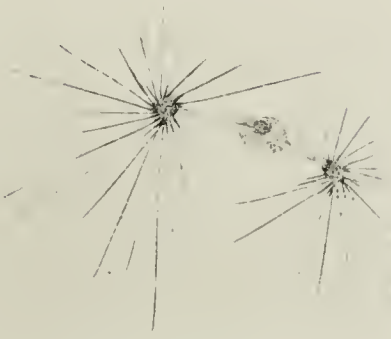

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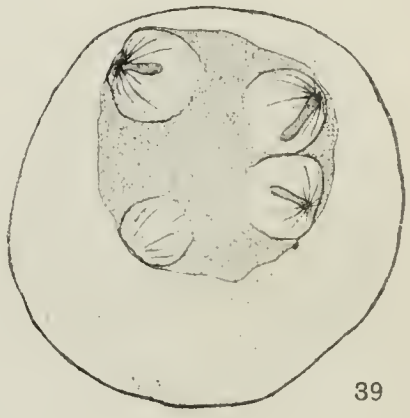

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PLATE 9.

Figs. 40–48, *Neotiella albocincta.*

Fig. 40. Mature one-nucleated stage of ascus.

Fig. 41. First spindle after cleavage of chromosomes. U-shaped chromosomes with very thick arms. Very fine astral rays.

Fig. 42. Somewhat older stage than represented in figure 41. Occasionally the long axis of the spindle is in a transverse plane, as it almost invariably is in *Urnula craterium.*

Fig. 43. Anaphase of first spindle stage. The arms of the chromosomes greatly lengthened.

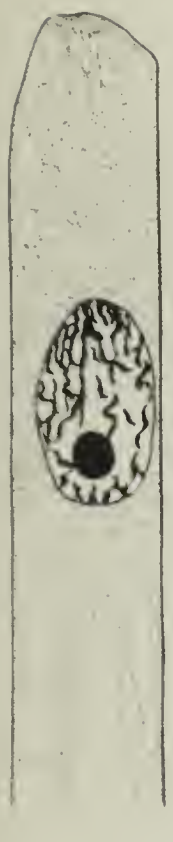
Fig. 44. Equatorial-plate stage of second mitosis. Nuclear wall unusually persistent.

Fig. 45. Late anaphase stage at end of third mitosis. Limiting layer probably beginning to form.

Fig. 46. Nuclear walls re-formed and already growing towards center of ascus. The limiting layer is complete.

Fig. 47. Spore initials have grown somewhat and nuclear beaks have nearly reached their maximum length.

Fig. 48. Plasma membranes almost half completed.



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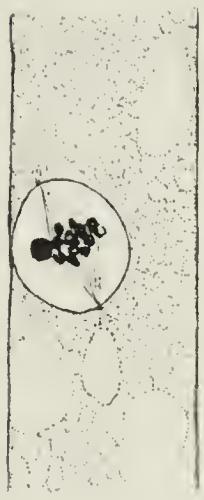

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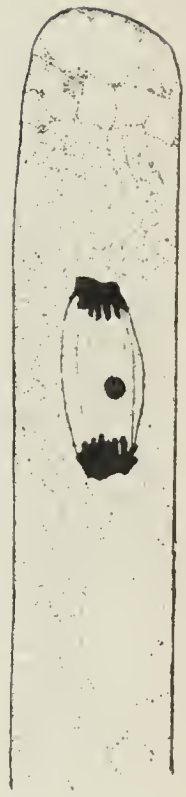

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PHOTOTYPE CO., BOSTON

PLATE 10.

Fig. 49–52, *Neotiella albocincta.*
Fig. 53–59, *Sordaria fimicola.*

Fig. 49. One of the spindles of last mitosis.
Fig. 50. Two spores in which the double plasma membranes are completed and shown slightly separated. The upper spore with two nuclei is a rare occurrence.
Fig. 51. Retraction of nuclear beak.
Fig. 52. Nucleus of a growing spore in resting condition.
Fig. 53. Four-nucleated stage of ascus at end of second mitosis. A centrosome outside of each nucleus.
Fig. 54. Last mitosis. Dense protoplasm quite vacuolated.
Fig. 55. Late anaphase stage of last mitosis. Spore plasm being differentiated and limiting layer forming.
Fig. 56. Limiting layer completed about each spore and nuclear wall formed.
Fig. 57. Plasma membrane is organized. Corresponding plasma membrane that covers cavity in epiplasm not represented in drawing.
Fig. 58. Karyokinesis in the spore.
Fig. 59. Binucleated spore.
Fig. 60. *Podospora zygospora.* Extranuclear bodies about the "fusion" nucleus.
Fig. 61. *Podospora curvula.* Extranuclear bodies as in figure 60.
Fig. 62. *P. curvula.* Nucleus has moved down to entrance of tail preparatory to forming a septum.
Fig. 63. *P. curvula.* Septum has been formed and nucleus has retired.

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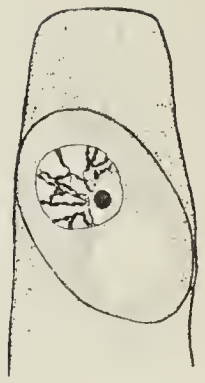
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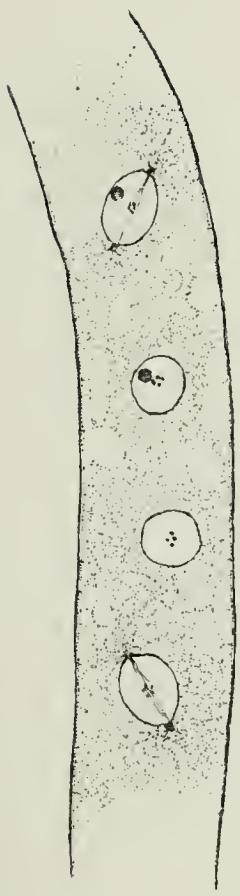
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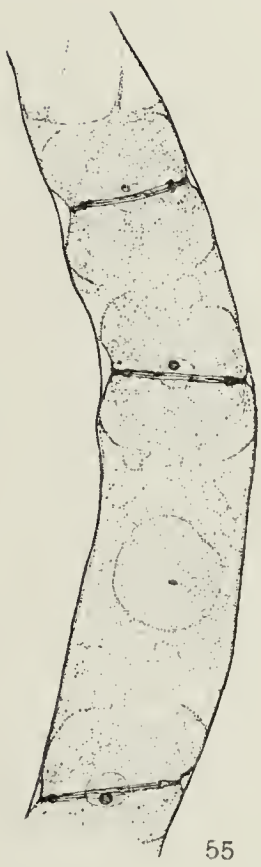
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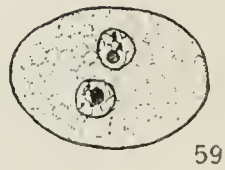
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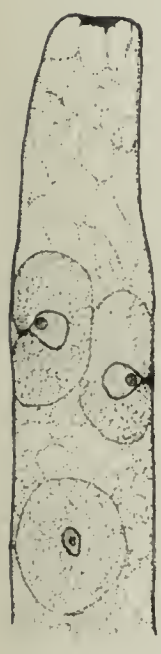
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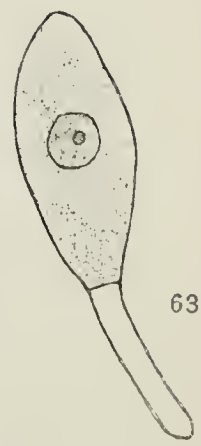
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HELIOTYPE CO. BOSTON

PLATE 11.

Fig. 64, *Peziza* sp.
Fig. 65–69, *Neotiella albocincta.*

Fig. 64. Nuclear division in hooked terminal cell of an ascogenous hypha prior to origin of ascus.
Fig. 65. One of the daughter nuclei of later stage than represented in figure 64 cut off by a septum from the rest.
Fig. 66. A second septum formed cutting off a nucleus and tip of hypha. The proximal cell seems to be preparing to form a new "hook."
Fig. 67. Fusion of nuclei in young ascus.
Fig. 68. Young ascus showing fusion nucleus.
Fig. 69. Fusion not yet effected, though ascus is growing out,— a frequent occurrence.
Fig. 70. Base of ascus of *Leptoglossum* sp.
Fig. 71. Base of an ascus of *Verpa bohemica.*
Fig. 72. Base of an ascus of *Verpa bohemica.*
Fig. 73. Base of an ascus of *Morchella esculenta.*
Fig. 74. Base of an ascus of *Genea hispidula.*
Fig. 75. Base of an ascus of *Verpa bohemica.*
Fig. 76. Base of an ascus of *Sordaria fimicola.*
Fig. 77. Base of an ascus of *Verpa bohemica.*
Fig. 78. Ascus of *Hydnobolites* sp.
Fig. 79. *Verpa bohemica*; showing base of ascus and end of ascogenous hypha.
Fig. 80. *Anixia spadicea*; showing base of ascus and ascogenous hypha.

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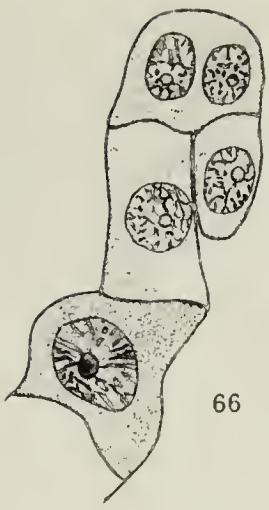
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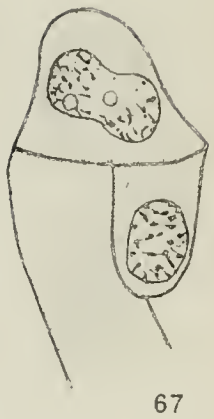
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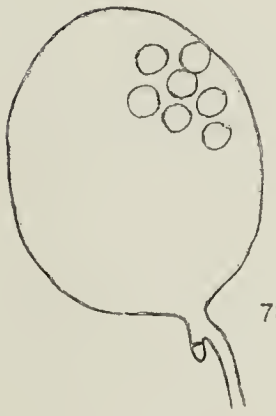
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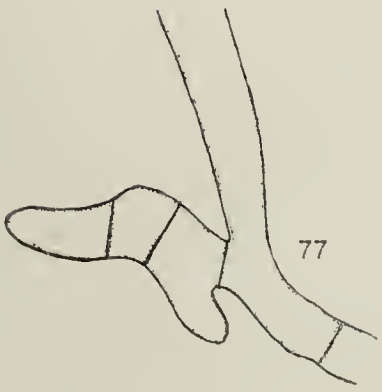
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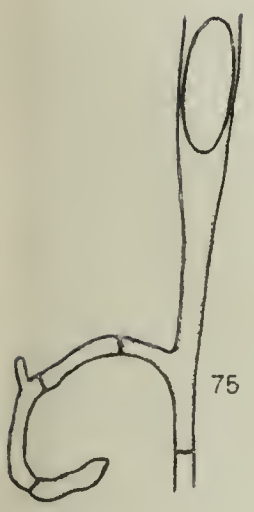
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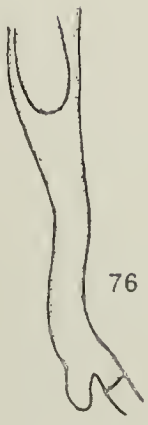
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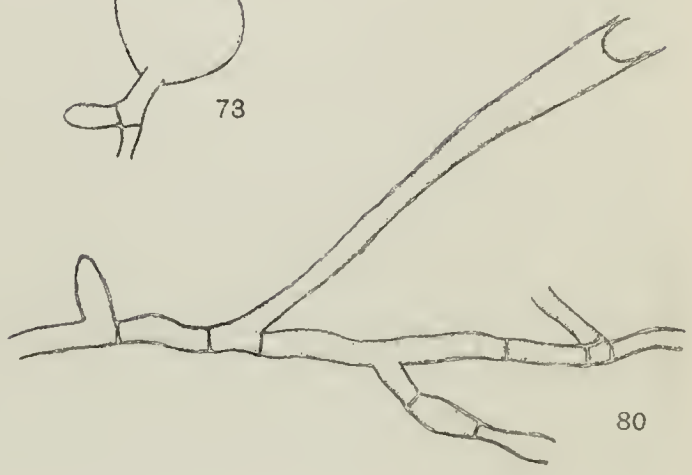
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HELIOTYPE CO. BOSTON

Proceedings of the Boston Society of Natural History.

Vol. 32, No. 5,

p. 115–143.

LIBRARY
NEW YORK
BOTANICAL
GARDEN.

PROCEEDINGS OF THE ANNUAL MEETING, MAY 3, 1905.

BOSTON:
PRINTED FOR THE SOCIETY.
June, 1905.

No. 5.— PROCEEDINGS OF THE ANNUAL MEETING, MAY 3, 1905.

REPORT OF THE CURATOR, CHARLES W. JOHNSON.

The plan for rearranging the collections referred to in the last annual report has in a great measure been carried out. The New England mammals and birds now occupy all the cases on the main floor of the museum with the exception of one case devoted to New England paleontology. This material will later be transferred to the horizontal cases in the room devoted to American paleontology.

All of the larger skeletons and one elephant have been removed from the main floor, and the other elephant placed upon the raised portion corresponding to the position of the Megatherium. These alterations give ample floor space for two cases for the larger New England mammals, and also room for a number of smaller cases for groups of birds.

The work on the main gallery has also progressed, but there is still a great deal to be done especially in arranging the fishes and insects.

Part of the Guide to the Invertebrata in the synoptic collection, by Mrs. J. M. Arms Sheldon, is still in press, but Part 1 (Protozoa, Porifera, Coelentera) and Part 2 (Echinoderma, Mollusca) have appeared. As soon as completed, a copy available to visitors will be placed with the collection.

Birds, Mammals, Reptiles, Batrachians.

There has been a very active interest taken in developing the collection of New England birds. Through the generosity of Mr. John E. Thayer the Society has received two very attractive and instructive groups. One shows the red-shouldered hawk feeding its young, and the other illustrates the social nesting habits of the black-crowned night heron. Mr. Thayer also presented the handsome case containing the latter group. Mr. Augustus Hemenway has donated twenty-seven species of New England birds, several of which were new to the collection, while others show special phases of plumage or replace poor specimens. Mr. Dwight Blaney pre-

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sented a beautiful pair of mallards, an American golden-eye, and a green-winged teal, all shot at Eastham, Mass. Other accessions are: a European goldfinch captured at the Charlestown navy yard by Mr. George Mayo; a handsome specimen of the little blue heron in adult plumage, which was obtained on Chappaquiddick Island, near Edgartown, Martha's Vineyard, April 14, 1904, and skins of the redhead and wood duck, from Mr. R. H. Howe, Jr.

Mr. C. E. Brown has continued his work on the New England collection, adding some sixteen species, including Leach's petrel, red-legged black duck, lesser scaup, Holboell's grebe, and snowy owl. He has also prepared nine groups representing the robin, least flycatcher, slate-colored junco, chipping sparrow, tree swallow, phoebe, bluebird, and black-capped chickadee. He has also remodeled the woodcock group and the groups prepared last season.

To the New England mammals have been added the doe of the northern Virginia deer, shot by Mr. Brown at Moosehead Lake; two deer heads from Aroostook County, Maine — one with abnormal antlers, the other a partial albino; a gray fox from Kent, Connecticut; meadow mouse from Moosehead Lake; and a little brown bat (*Myotis lucifugus*) from Intervale, N. H., the last collected by Dr. G. M. Allen. The model of the white whale has been recolored and placed on the main floor.

The Society has received a copperhead from the Blue Hills, from Mr. Roland Hayward; a number of reptiles and batrachians collected in Rhode Island, from Mr. R. H. Howe, Jr.; several reptiles from Mr. Owen Bryant; and a black snake from Mr. B. Grover. A large portion of the New England birds, and all of the mammals, reptiles, and batrachians have been relabeled.

Insects, Crustaceans.

Many of the members of the Society and of the Cambridge entomological club have contributed largely to the New England collection of insects. Dr. F. W. Russell, of Winchendon, has presented 456 specimens of moths, among them many rare and interesting species, also a number of Hymenoptera and Diptera; Mr. L. W. Swett 85 specimens of moths and butterflies; Mr. C. A. Frost upwards of 275 specimens, representing several orders; Mr. Roland Hayward 22 species of Carabidae; Mr. A. P. Morse a number

of Diptera and Hemiptera, and an interesting example showing the destructive work of the "powder post" (*Lyctus striatus*). Mr. Owen Bryant has continued his active field work and added very materially to the collection. Mr. S. A. Shaw, of Hampton, N. H., has contributed about 50 species of Diptera; Mr. F. H. Foster, of Claremont, N. H., 24 specimens of *Haploa confusa* representing the parents and progeny, an excellent illustration of specific variation; and Dr. G. M. Allen a number of desirable dragon flies and other insects from the White Mountains. Specimens have also been received from Messrs. C. V. Blackburn, Dwight Blaney, F. C. Bowditch, J. A. Cushman, N. S. Easton, J. H. Emerton, Abner Hatfield, Samuel Henshaw, H. H. Newcomb, J. H. Rogers, Jr., F. A. Sherriff, and J. D. Willard, and from Mrs. J. F. Stevens and Miss Caroline G. Soule.

During the latter part of June and early July the Curator visited the Cape Cod region, collecting at Provincetown, Eastham, Chatham, Hyannisport, and Barnstable. About 2000 specimens were collected. In the vicinity of Boston over 2500 additional specimens were obtained during the season. These are being incorporated in the collection as the various groups are studied. Through a generous contribution from Miss Susannah Minns, preliminary measures have been taken towards investigating the mosquitoes of eastern Massachusetts. Miss Martin has made a number of drawings of the Culicidae and other insects.

To the exhibition collection have been added thirty glass-covered boxes (14 × 22 inches), while in the study collection eighty Schmitt boxes have been arranged, including sixty of Coleoptera, twelve of the Neuropteroid insects, determined through the kindness of Mr. Nathan Banks, and eight of Hymenoptera determined by Mr. H. L. Viereck. Mr. J. H. Emerton has revised the names and assisted in rearranging the collection of mounted spiders.

Miss Mary J. Rathbun and Prof. C. B. Wilson have kindly determined several species of Crustacea. The Society has received from the United States national museum twenty-two species, sixty specimens, of New England Crustacea. A number of species were collected by the Curator at Chatham, and by Mr. Cushman at Manomet. The Crustacea have been labeled and arranged in the railing cases on the main gallery. Mr. Cushman has also studied and relabeled the general collection of barnacles.

Molluscs.

The New England collection, which has been relabeled and placed in special trays, has been largely augmented through the liberality of Mr. Dwight Blaney who has donated 101 species, 1070 specimens dredged in Frenchman's Bay, Maine, and 23 species (about 200 specimens) from various places on the Massachusetts coast. Dr. C. W. Townsend presented seven species dredged off Northeast Harbor, Maine; Mr. Abner Hatfield a fine series of *Sipho stimpsoni* and *Buccinum undatum* showing considerable variation; Mrs. A. S. Packard a large and interesting series of *Helix hortensis* from Brown Cow Island, Casco Bay, and from various other localities; also a series of *Io spinosa* from the Houlston, Clinch, and Tennessee Rivers. Specimens have also been received from Messrs. Owen Bryant, J. A. Cushman, and the Curator.

The work of revising the general collection has been continued. The Mayo collection is being classified and incorporated, and some 1350 species have been catalogued and numbered by Miss Martin, who has also cleaned and remounted all those reserved for exhibition. In revising the Pelecypoda the Curator has had valuable assistance from Mr. Cushman who has labeled and arranged thus far about two thirds of this group. Twenty-five species of shells from Nicaragua were presented by Rev. W. H. Fluck.

Echinoderms, Corals, etc.

The general collection of echinoderms and coelenterates has been rearranged and labeled by Mr. Cushman, and all the types carefully studied and designated. A number of fine corals were added to the collection, including twelve species obtained from Mr. Abner Hatfield in exchange, also one from Mr. J. H. Holmes, and one from Miss A. P. Loving. Some alcoholic material was obtained from Mr. Dwight Blaney.

The New England Coelenterata, Porifera, and part of the Protozoa, have been arranged. The Hydrozoa and Foraminifera are shown by enlarged illustrations and drawings.

The collection of microscopic slides has been studied by several members, and some of the results published in the American natu-

ralist for April. An additional label bearing the name of the Society is being placed on all slides to avoid a possibility of their being lost.

Paleontology.

The work in this department has been largely that of rearranging and condensing so as to give more space to the New England birds. The types in the Eser collection of foreign fossils, have as far as possible been catalogued and indicated on the label. Mr. Cushman again visited Gay Head and obtained a large number of fossils, especially crustaceans. The results of a study of these will shortly be published by him in the American naturalist with figures. A single specimen of *Cancer proavitus* Packard was obtained. The type of this species has recently been presented to the Society by Mrs. A. S. Packard. The Devonian plants from Perry, Maine, have been studied by Dr. David White, resulting in one new species, and the discovery of a type. The type of *Gennaeocrinus carinatus* Wood, has been received from the Massachusetts institute of technology in exchange for material for class work. A series of lower Cambrian fossils from Weymouth, Mass., was received from the Paleontological department of Harvard university.

Botany.

Miss Carter has continued her work of revising the herbarium, having finished the Polypetalous group, which is represented by 6259 species and 10,960 specimens. The Caprifoliaceae, Rubiaceae, Dipsacaceae, and part of the Compositae have also been studied. Miss Susannah Minns has presented 300 specimens, chiefly White Mountain plants and western grasses. Seventeen persons have consulted the collection.

There has been a marked increase in the number of visitors to the museum on public days, while on other days it has been visited by 362 pupils representing 14 schools. Material for study has been loaned to nineteen persons.

REPORT OF THE SECRETARY AND LIBRARIAN, GLOVER M. ALLEN.

Membership.

During the year 1904–1905, the Society has lost by death one Honorary Member — Adolph Bastian — and three Corresponding Members — Auguste de Jolis, E. J. Marey, Robert McLachlan. Seven Corporate Members also have died during the year — Samuel L. Abbot, James M. Barnard, Edward W. Codman, F. W. G. May, Alpheus S. Packard, Frances C. Prince, Eleanor P. Rathbun. James M. Barnard was also a Patron of the Society. Thirteen Corporate Members have resigned.

Seven new Honorary Members have been elected by the Council — Edouard Bornet, William Boyd Dawkins, Sir Archibald Geikie, Karl F. Goebel, Angelo Mosso, Sir John Murray, Ferdinand von Richthofen. Four new Corresponding Members also were elected — T. C. Chamberlain, Charles R. Van Hise, William Libbey, Albrecht Penck.

Eleven new Corporate Members have been elected during the year. The names of these new members and the dates of their election are as follows: —

William E. Castle, October 14, 1904.
Jesse M. Greenman, October 14, 1904.
William P. Henderson, December 16, 1904.
Harry G. Higbee, October 14, 1904.
Edward G. Humphrey, December 16, 1904.
Robert G. Leavitt, October 14, 1904.
Frank R. Lillie, October 14, 1904.
George Mayo, December 16, 1904.
Edward Reynolds, M. D., October 14, 1904.
Irving L. Shaw, October 14, 1904.
Charles W. Townsend, M. D., October 14, 1904.

The net loss in the number of Corporate Members is nine. The corrected list of members, May 1, 1905, shows a total of 14 Honorary, 116 Corresponding, and 456 Corporate Members, a total membership of 586, or five less than last year. There are 14 Patrons.

Meetings.

Fourteen regular meetings of the Society have been held during the year. The number of persons present at any one meeting has varied from 26 to 118, the average attendance being about 51, as against 55 for last year.

The total attendance for the year is 707. Fifteen formal communications have been made during the year by as many persons, of whom eleven had not previously spoken before the Society. Eight papers have been presented by title.

The meetings, attendance, and communications have been as follows: —

May 4, 1904. Annual meeting. Twenty-eight persons present.

Reports of the Curator, Curator of the Teachers' school of science, Secretary, Librarian, Treasurer, Trustees.

Mr. C. W. Johnson. Brief remarks on the exhibition of the Mollusca in the Society's collection.

Mr. F. N. Balch. The Nudibranch Mollusca of New England,

May 18, 1904. General meeting. Thirty persons present.

Mr. Glover M. Allen. The Newfoundland whale fishery.

Prof. George E. Stone. The influence of current electricity on plants. (By title.)

November 2, 1904. General meeting. Forty-eight persons present.

Prof. William M. Davis. Physiographic notes in Colorado, Utah, and Mexico, 1904.

Prof. Edward C. Jeffrey. The comparative anatomy and phylogeny of the Coniferales.— Part 2. The Abietineae. (By title.)

Dr. Millett T. Thompson. The morphology and metamorphosis of the alimentary tract of the mosquito. (By title.)

Miss Ellen Tucker Emerson, 2d. The general anatomy of *Typhlomolge rathbuni*. (By title.)

November 16, 1904. General meeting. Forty-one persons present.

Dr. Edmund D. Spear. How birds fly.

December 7, 1904. General meeting. Thirty persons present.

Dr. Douglas W. Johnson. A problem in river capture.

Mr. J. H. Faull. Development of ascus and spore formation in Ascomycetes. (By title.)

December 21, 1904. General meeting. Fifty-five persons present.

Prof. Stephen P. Sharples. Four months on a coral island in the Caribbean Sea.

January 4, 1905. General meeting. Twenty-six persons present.

Dr. George W. Cutler. Sponge fisheries in the Bahamas.

January 18, 1905. General meeting. Seventy-one persons present.

Mr. Ernest Harold Baynes. Our last chance to save the buffalo — an appeal for the preservation of our finest native mammal.

February 1, 1905. General meeting. Forty-three persons present.

Prof. R. T. Jackson. Evidence for evolution amongst fossil invertebrates.

February 15, 1905. General meeting. Thirty-five persons present.

Mr. Frederic A. Lucas. The taking and the making of a whale; an account of the capture of a sulphur-bottom whale, and the preparation of a life-sized model.

Mr. Fred Mutchler. The structure and biology of the yeast plant. (By title.)

March 1, 1904. General meeting. Thirty-one persons present.

Prof. John S. Kingsley. The lower jaw of mammals.

March 15, 1905. General meeting. One hundred and eighteen persons present.

Mr. François E. Matthes. The cliffs of the Grand Canyon.

Dr. S. R. Williams. The anatomy of *Boophilus annulatus* Say. (By title.)

Mr. James A. G. Rehn. Systematic results of the study of North American land mammals during the years 1903 and 1904. (By title.)

April 5, 1905. General meeting. Seventy-five persons present.

Mr. Alfred E. Preble. Down the Mackenzie in a canoe.

April 26, 1905. General meeting. Seventy-six persons present.

Prof. George H. Barton. Hawaii, its scenery, volcanoes, and people.

Publications.

During the year the following publications have been issued: —

The comparative anatomy and phylogeny of the Coniferales. Part 2. — The Abietineae. By Edward C. Jeffrey. Memoirs, vol. 6, no. 1, 37 pages, 7 plates.

Title pages and index to Memoirs, vol. 5.

Pycnogonida collected at Bermuda in the summer of 1903. By Leon J. Cole. Proceedings, vol. 31, no. 8, 14 pages, 3 plates.

North American Ustilagineae. By G. P. Clinton. Proceedings, vol. 31, no. 9, 201 pages.

The anatomy and development of the terrestrial nemertean (*Geonemertes agricola*) of Bermuda. By Wesley R. Coe. Proceedings, vol. 31, no. 10, 40 pages, 3 plates.

Title pages and contents of Proceedings, vol. 31.

Proceedings of the Annual Meeting, May 4, 1904. Proceedings vol. 32, no. 1, 21 pages.

List of shell-bearing Mollusca of Frenchman's Bay, Maine. By Dwight Blaney. Proceedings, vol. 32, no. 2, 19 pages, 1 plate.

General anatomy of *Typhlomolge rathbuni*. By Ellen Tucker Emerson, 2d. Proceedings, vol. 32, no. 3, 34 pages, 5 plates.

Under the editorship of Mr. Samuel Henshaw, there have also been issued parts 3 and 4 of volume 7 of the Occasional Papers devoted to the Fauna of New England. These two parts comprise respectively the List of the Mammalia, 35 pages, and the List of the Echinodermata, 13 pages.

Library.

The additions to the library during the year have been as follows: —

	8vo.	4to.	Folio.	Total.
Volumes	319	60	14	393
Parts of volumes	1707	307	10	2024
Pamphlets	592	32	14	638
Maps			17	17
Total	2618	399	55	3072

Thirty-one volumes of the library of Prof. A. S. Packard have been presented by his son, Mr. A. A. Packard, to the Society's library. We have also received from Mr. Charles S. Fellows, a complete copy of the original edition of C. L. Koch's Deutschlands crustaceen.

The cataloguing of the S. H. Scudder library is finished, the maps only remaining to be done. About 2000 of the pamphlets have still to be prepared for the shelves.

Two exchanges have been added during the year, *viz.*, Bulletin scientifique de la France et de la Belgique and Université de Rennes, Travaux scientifiques. One exchange has ceased (Wagner Free Institute). The exchanges number 455.

During the year 238 volumes have been bound. Eight hundred and twenty-two volumes have been borrowed by 114 persons; 358 books have been borrowed for use in the building. The library has been consulted about 340 times.

The library contains, May 1, 1905, 31,264 volumes (1445 current or otherwise incomplete volumes) and 23,873 pamphlets.

REPORT OF THE TREASURER, EDWARD T. BOUVÉ.

Annual Statement, May 3, 1905.

1904, May 1	To balance April 30, 1904, belonging to			1905, Apr. 30	By cash paid for	
	Library	224.49			Fuel and Light	$484.08
	Museum	436.18			General Expense	860.39
	Publications	436.09			Insurance	118.00
	General Expense	998.55	$2095.31		Museum	1016.50
1905, Apr. 30	To cash received from income,				Library	1383.38
	General Fund		5154.77		Publications	2621.08
	Bulfinch Fund		1715.50		Salaries	7580.00
	Flint Fund		204.11		Walker Prize Adv	49.50
	Pratt Fund		559.18		Walker Prizes	100.00
	Wolcott Fund		398.67		Janitor Services Lecture Hall renting	24.00
	Saltonstall Fund		981.41		Repairs	30.19
	Waterston Fund		452.96	" "	Trustees for Ins. Sinking Fund	543.00
	Walker Fund		1961.70	" "	"	684.46
	Randall Fund		250.00		Balance carried to new account (this belongs to General Expense Account)	1648.16
	Billings Fund		805.00			
	Special Museum		110.25			
	Mass. Inst. Technology		200.00			
	Admission Fees		70.00			
	Annual Assessments		1615.00			
	Museum Fees		127.00			
	Sales of Publications		261.12			
	Rent of Lecture Hall		133.00			
	Interest on deposit Shawmut Bank		46.21			
	Library Remittance returned		1.55			
	Total,		$17,142.74		Total,	$17,142.74

TEACHERS' SCHOOL OF SCIENCE.

1904, May 1	To balance from old account		$36.34	1905, Apr. 30	By cash paid for Lectures and Supplies	$2818.56
1905, Apr. 30	To cash received from A. L. Lowell, Trustee		2385.53		By balance to new account	14.27
" "	" " " Donation		400.00			
	Interest on deposit Shawmut Bank		10.96			
	Total,		$2832.83		Total,	$2832.83

ARMS FUND.

1904, May 1	To balance from old account		$1740.34	1905, Apr. 30	By balance to new account	$1780.39
1905, Apr. 30	Petty cash returned		5.25			
	Interest on deposit Shawmut Bank		34.80			
	Total,		$1780.39		Total,	$1780.39

ABSTRACT OF REPORT ON THE TEACHERS' SCHOOL OF SCIENCE, BY PROF. G. H. BARTON, CURATOR OF THE SCHOOL.

During the year the usual field and laboratory courses have been given.

The field courses in botany, under the charge of Mr. Hollis Webster, were especially devoted to a study of the bryophytes and the pteridophytes. The average attendance during the spring lessons was 31, and during the autumn lessons, 30.

The field work in zoology, under Mr. A. P. Morse, was directed largely to observation of the animals studied in the winter,— crustaceans and insects. The average attendance at the spring lessons was 30, and at the autumn lessons, 16.

The course in field geology is not a Lowell course, but is supported by a friend of the School. It is given by the Curator of the School with the aid of one or two competent assistants. The lessons this year were devoted mostly to a study of the lithological character of the rocks near Boston in continuation of the laboratory work of the preceding winter. The average attendance at the spring lessons was about 47, and in the autumn, 42.

The laboratory course in botany, given by Mr. Hollis Webster with the assistance of Miss J. F. Conant, was directed to a study of the flowering plants, and was supplemented by lectures on the life history and morphology of gymnosperms and angiosperms. The average attendance for the term was about 40. This year's work finishes the four years' course and about twenty diplomas will be granted.

The laboratory work in zoology was devoted this year to a special study of insects. This course is given by Mr. A. P. Morse with the assistance of Miss M. E. Cherrington. The average attendance was about 32.

The laboratory course in geology is given by the Curator of the School. Two classes are now for the first time carried on. The advanced class took up dynamical and structural geology and showed an average attendance of about 72. Eight of the pupils, having finished the four years' course, will receive diplomas this year. The beginners' class took up the subject of mineralogy. The average attendance was about 59, and the final examination was taken by 32.

In addition to the work on Saturdays each class has met one evening per week for general discussion. The average attendance for the winter was about 29. The average attendance for the combined classes in geology was therefore 160.

During the summer, the Curator of the School conducted a party of teachers on a geological trip to the western United States and the Hawaiian Islands. Ten made the entire trip while others accompanied the party to various points in the west.

In addition to this work, the Curator of the School has spoken before pupils and teachers of sixteen schools about Boston.

Through the personal efforts of Mr. Hollis Webster, fifty new dissecting microscopes have been added to the School's equipment.

A special course of eight lectures, each by an authority on his subject, has been given during the winter. These lectures were held at Huntington Hall and were largely attended.

It was voted that these reports be accepted and placed on file.

The report of the Trustees was accepted and placed on file.

Prof. R. T. Jackson reported for the Walker Prize committee that seven manuscripts had been submitted in competition for the two annual prizes. On the recommendation of the committee it was voted that a Walker first prize of $75 be awarded to the author of the memoir entitled "A physiological analysis of the phenomena of regeneration in plants" and a Walker second prize of $50 to the author of the memoir entitled "Quaternary correlations along the New York and southern New England coasts."

The envelopes containing the names of the successful competitors were then opened by the President, who announced that the winner of the first prize was W. B. McCallum of the University of Chicago, and the winner of the second prize was M. L. Fuller of the United States geological survey.

The Society then proceeded to elect officers for the ensuing year. The President appointed Mr. J. Henry Blake and Prof. George H. Barton to act as tellers. After the ballots had been collected and counted, it was announced that the following candidates were duly elected.

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ALIMENTARY CANAL OF THE MOSQUITO.

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No. 6.—ALIMENTARY CANAL OF THE MOSQUITO.[1]

BY MILLETT T. THOMPSON.

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Introduction.

Literature on the mosquitoes is rather extensive, especially that which deals with the genus Anopheles. Comparatively few articles, however, discuss the internal anatomy of these flies and in many of those papers where details of internal structure are given, these are not cited from morphological motive. The structure of the salivary glands or the alimentary canal may be described, but it is to make clear the life history of the malarial Plasmodium or as a guide in dissecting when studying these parasites, and not from interest in the anatomy itself. In view of the secondary purpose of such descriptions it has not seemed best in this paper to make a complete survey of articles of this class or to comment at length on the interpretations of structure that are presented. Criticism and discussion will be limited to the few researches which deal extensively with the internal anatomy or which discuss this from a morphological view-point.

Of the studies that fall into this last group, several are found which give accounts of Anopheles. Nuttall and Shipley's, "The structure and biology of Anopheles" and Christophers' "The anatomy and histology of the adult female mosquito" are comprehensive and very valuable. Annett and Dutton's "Report" is excellent but more limited in scope. As far as anatomical details are concerned at least, Giles' "Handbook of the gnats or mosquitoes" is unreliable. I have been unable to obtain Grandpré and Charmoy's "Les moustiques." With respect to Culex on the other hand, I know of no single comprehensive work, but scattered descriptions of the various internal organs exist. The external form of the larvae and pupae of mosquitoes has been studied considerably, but the internal anatomy of these stages has been neglected. Raschke gives the best account for the larva in "Die larve von *Culex nemorosus*." Our knowledge of the metamorphosis of the internal organs

[1] From the Biological laboratory, Clark university, and the Laboratory of the U. S. bureau of fisheries, Woods Hole, Mass.

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is summed up in two excellent papers by Hurst, "The pupal stage of Culex" and "The post-embryonic development of a gnat," and in details given by Miall and Hammond ('92) from Hurst's unpublished notes.

Three species of Culex as they occurred at different seasons furnished the material on which this paper is based. *C. stimulans* and *C. pipiens* were used for the study of the perfect insect, and a small midsummer form that was not identified gave me larvae and pupae. Comparative notes were made at all stages, but failed to bring out appreciable differences between the three forms at any time. The genus Culex was used instead of the more important Anopheles, because early in the study it became impossible to obtain a sufficient number of specimens of the latter, either larvae or adults. However, enough material was available to enable me to compare the two genera with respect to many structures and to check the descriptions given in the literature dealing exclusively with Anopheles. The specimens of Anopheles at my disposal were representatives of the commonest New England species, *A. punctipennis*.

Technique.

The chitin of the imago of the mosquito is not heavy enough to offer especial obstacles to research, except as it interferes with the penetration of the killing fluids. This was overcome without injury to important structures by cutting off the dorsum of the thorax while the insect was immersed in the reagent. Of all killing fluids that were tried, Gilson's mercuric nitrate proved most valuable, and in the end was exclusively used. In order to remove air from the scales, the mosquito was dipped for a moment in alcohol before it was plunged into the warm fluid. I made Gilson's fluid according to the following formula: —

70 % alcohol	10	parts.
Distilled water	86	"
Corrosive sublimate (crystals)	2	"
Glacial acetic acid	½	"
Nitric acid (80 %)	1½	"

Dissection is of primary importance in a study of the thoracic and abdominal portions of the alimentary canal of the mosquito. But

it must be constantly controlled and supplemented by sections. Knowledge of the structures within the head of the insect on the other hand, has to be derived almost wholly from sections. Reconstruction proved of slight value. I used serial sections cut in the three planes usually employed and depended on careful study of these, adding to and controlling the interpretations by study of dissections and of material cleared with caustic. Excellent thick sections — 30 μ or over — for control and demonstration were prepared by killing in Flemming's fluid and allowing the specimens to blacken somewhat. Material treated thus may be imbedded in paraffin, sectioned, and the sections mounted without staining. The discoloration produced by the killing fluid gives sufficient character to the structures.

With the larva of the mosquito, study of the living animal or of fresh dissections is of paramount importance. Sections of the head especially are not readily interpretable taken alone. Fortunately for research, the wriggler of Culex has a large, transparent head, so that the contained structures can easily be made out in the living animal or in whole mounts of the head. In the light of knowledge obtained in this way, sections become interpretable and through these in turn we are enabled to understand sections of the Anopheles wriggler, where the head is small and opaque. An excellent method for mounting the whole head is to stain with picro-carmine and then clear through Weigert's fluid. Fine preparations may also be obtained by staining with haematoxylin, but this method is slower and less uniformly successful than the picro-carmine stain.

The pupa stage can only be studied from serial sections and to work to best advantage a series of specimens the ages of which are approximately known, is needed. Such a series was obtained for Culex by segregating mature larvae in a dish and each hour removing all pupae to separate containers, in which they could be reared for any desired number of hours. A very complete series ought to be obtained. In the summer our species of Culex spend from 48 to 70 hours as pupae, and I did not find that a set of specimens representing in ages nearly every hour up to the thirtieth of pupal life and then more distant intervals, was too extensive.

Imago.

Head and mouthparts. — An extended description of the external anatomy of the mosquito does not come within the scope of this paper. A few points with respect to the head, however, must be noted. The part of the head that lies in front of the large compound eyes is inflated above to form a rectangular box, which is called the clypeus. This seems to correspond to the "face" of other flies. A vertical furrow is impressed into the anterior face of this box. At the foot of the furrow a boss of chitin for muscle insertion projects into the cavity of the clypeus, while near the roof of the box on either side a short chitinous ala also enters the cavity. Ventrally and at the sides, the pre-ocular region of the head is rounded and forms as it were an imperfect cylinder, at the summit of which the mouthparts arise, nearly at one level. The anterior wall of the clypeus lies forward of this point by one half of the length of the box in the female insect and nearly two thirds of the length in the male. The postocular or epicranial region of the head is extensive in the female but truncate in the male mosquito.

Within, the head is strengthened by a mesial crest which continues from the level of the antennae along the roof of the head to the border of the occipital foramen. It is also braced by two hollow cylindrical struts which pass from the ventral border of the occipital foramen to the cheeks. I shall refer to these struts as tentoria, without intending to imply any necessary morphological connection between them and the analogous internal head braces of other insects. Among the flies, hollow tentoria similar to those of the mosquito are found in Chironomus, Anopheles, and Simulium. They appear to be wanting in many families, as, for example, the Tipulidae, Asilidae, Dolichopodidae, and the Muscidea. The Tabanid flies have solid tentoria with somewhat the same relations as the hollow struts of the mosquito. In the female of Culex the tentoria arise in front of the border of the occipital foramen and ascend at an angle of twenty-five degrees with the floor of the head. Each strut has a short spur near the lower end, to which no obvious function can be assigned, and above as the cheeks are approached, flares out into an irregular funnel-shaped "head." In the male mosquito the struts arise from the border of the occipital foramen, and the

differently shaped head makes the angle with the floor measure nearly thirty-five degrees. The struts are provided with the seemingly useless spur near the foot, but above expand suddenly to form the "head" and then the tube narrows again as it meets the cheeks.

The mouthparts (pl. 16, fig. 46–47) of the mosquito need no elaborate description here. The usually accepted nomenclature will be employed for the various stylets. The labrum is horseshoe-shaped in section and forms the whole or the major part of the tube (*pc*) through which the insect sucks blood or other liquid. There is no good reason to retain the name labrum-epipharynx for this dorsal stylet, with the consequent implication that the organ is compound. Becher long ago ('82) pointed out that the separation into two parts under manipulation was an artifact. Morphologically for the imago of Culex (pl. 16, fig. 46–47) and for the imagoes of other flies (Kräpelin, '82, '83) the labrum is a unitary structure. During the metamorphosis of Culex also, the labrum is formed as a simple tube. The canal (*pc*) on its ventral face is moulded by the infolding of the ventral wall. The labrum receives a single muscle which probably serves for a retractor and depressor. This muscle is inserted on the boss of chitin at the base of the labrum and its fibers arise from the dorsal and posterior walls of the clypeus. It may be called the labral muscle (pl. 12, fig. 2). This muscle has been described as "labral muscle" (Annett and Dutton, :01), "elevator of labrum-epipharynx" (Nuttall and Shipley, :01–:03), "retractor of labrum" (Giles, :02), and "retractor partes productae" (Meinert, '81). It corresponds in part to the "pharyngeal muscle" of Dimmock ('81).

The mandibles are wanting in the male mosquito and are slender, delicate lancets in the female. Dimmock ('81) has figured these organs in the cross section of the mouthparts as lying beneath the hypopharynx. Giles (:02) gives a similar arrangement in one figure while in another he shows the mandibles above the hypopharynx at the sides of the labrum. This last is the proper position for the stylets when at rest. The mandibles are morphologically dorsal to the hypopharynx. The other position is due to misplacement during the processes of sectioning. Each mandible is retracted by a mandibular muscle (*mnd m*) which arises on the "head" of the tentorium and is inserted on the base of the stylet. As these muscles approach their insertions short fibers connect them with the

adjacent walls of the head, but I am not certain whether the muscle is augmented by these fibers or instead partially inserts on the wall of the head.

The maxillae of the male mosquito are no stronger than the mandibles of the female, but the maxillae of the latter sex are powerful cutting lancets, armed near the apex with recurved teeth along the outer border of the blade. This border is thin and its chitinous cuticle is delicate. The inner border of the blade is broad and its chitin is thick (pl. 16, fig. 47). Proximally, the inner border terminates with an articular spur. From the point where the palp and the outer border of the maxilla blade unite, an apodeme enters the head and extends almost to the occipital foramen (pl. 12, fig. 2, *apo*). The maxillae have a complex musculature which must ensure a considerable freedom of movement, although it is possible to assign functions to the different muscles only in a general way (pl. 12, fig. 2; pl. 13). The most prominent muscle in sections lies parallel to and outside of the maxillary apodeme. It arises from the under side of the lower end of the tentorium and the adjacent walls of the head and is inserted on the base of the palp and apodeme. While the general action of the muscle must be the retraction of the maxilla, it would seem that it will also tend to divaricate maxilla and palpus. To adopt Dimmock's ('81) and Nuttall and Shipley's (: 01– : 03) name, this muscle is the retractor of the maxilla. Another important muscle arises from the "head" of the tentorium and is inserted on the articular spur of the maxilla. As it also sends fibers to the dorsal angles of the base of the labium, I call this muscle the double retractor. From its position it is probably the chief retractor of the maxilla blade, which cuts on the up stroke. It has an extensive tracheal supply.

Two pairs of muscles are found which probably serve to protract the maxillae. The larger of these, the protractors of the maxillae, are inserted on the free ends of the apodemes (*prot max*) and extend forward, inward, and upward to the tentoria. The origin is from the under surface of the strut just below the "head." The smaller pair of muscles, the maxillo-labials (*max-li*), are inserted towards the ends of the apodemes, and run forward along the inner side of the apodemes to the ventral border of the labium. In addition to these larger muscles, each maxilla receives on the articular spur a short band of fibers from the adjacent wall of the pharynx. Per-

haps these maxillary muscles counteract the divergent pull of the retractors of the maxilla. The retractors of the maxilla were described by Annett and Dutton (:01) as "muscle attaching maxillary process to occipital region of the skull." Possibly the double retractor is to be seen in Meinert's "retractor scalpelli" ('81, fig. 15). In the same figure the "protractor scalpelli" may represent the protractor of the maxilla. This protractor is described by Annett and Dutton and figured in figure 1, plate 18, but is not named. The maxillo-labial muscle is described by Annett and Dutton as "muscle to base of labium." It is less readily traced in other studies and may be either the "protractor scalpelli" or the "retractor scuti ventralis" of Meinert ('81, fig. 16), while it is possible that the muscle represented in figure 1, plate 8, of Nuttall and Shipley's account under the name "protractor maxilla" represents it. I have not found any muscle that will answer to Meinert's "retractor scalpelli" as shown in his figure 16.

The hypopharynx has a central "body," the mid-dorsal line of which is traversed by the salivary gutter, and thin lateral "wings." The hypopharynx is continuous with the labium at its first appearance in the pupa (Hurst, '90) and never becomes a separate stylet in the male insect, so that the salivary gutter traverses the dorsal face of the labium. At the base of the hypopharynx, the salivary gutter becomes continuous with the salivary pump, or as it is more often termed, the "receptacle of the salivary duct." This pump (pl. 12, fig. 1) consists of a chitin-lined cup, open above and in front into the salivary gutter, and closed behind with a plate of thin chitin overlaid by a mass of cells. This plate furnishes insertion for two muscles and is pierced by the orifice of the salivary duct. When the muscles attached to the plate contract, they draw the plate back, out of the cup, and saliva can flow in from the salivary duct. On their relaxation, the elasticity of the chitin causes the plate to re-enter the cup, forcing the contained saliva along the salivary gutter into the wound. Nuttall and Shipley (:01–:03) and Annett and Dutton (:01) have carefully described the similar pump of Anopheles. In *A. punctipennis* the pump appears to be of the same size as that of Culex in specimens of similar length. The hypopharynx receives muscle fibers from the mandibular muscles. The muscles which operate the salivary pump, the hypopharyngeal muscles, will be described in connection with the pharynx.

The labium, the largest of the mouthparts, is cylindrical, with a deep furrow along the dorsal surface. It terminates in a median ligula and two lateral labellae. The labellae are moved by small muscles, labellar muscles (Annett and Dutton, :01), from the walls of the distal part of the labium itself. The organ as a whole is not well provided with muscles. Proximally, the dorsal angles where it meets the head, receive fibers from the double retractor muscles and on the ventral border the maxillo-labial muscles arise. It is probable that the return of this organ to position after the displacement during blood sucking, is accomplished without the activity of muscles. The lumen of the labium is traversed by the two labial tracheae and by two nerves (*li n*) derived from the infra-esophageal ganglion of the brain.

The remaining muscles of the head fall into two groups: those associated with the various parts of the alimentary canal, and those supplying other organs. The former class will be discussed in connection with the parts of the alimentary canal which they supply. The latter group may be briefly noted. Each antenna receives scattered fibers from the frons and two large muscles from the "head" of the tentorium. One of these, the inner antennal muscle, is inserted on the inner angle of the base of the antenna. On contraction it must tilt the antenna forward and inward. The other muscle, the outer antennal muscle, is inserted on the outer posterior angle of the base of the antenna and hence on contraction must tilt the antenna backward and outward. This muscle is especially large in the male mosquito. On the outer face of either tentorium is inserted a slender muscle which enters the head through the occipital foramen. The muscles of this pair may be called the tentorial muscles and they correspond to a muscle labeled "retractor of the maxilla" by Nuttall and Shipley in their figure 23 on plate 8, and to the "salivary muscle" of Christophers (:01). The "retractor maxillae" in the remaining figures given by Nuttall and Shipley is the retractor of the maxilla of my series. The subocular muscles are a pair of minute muscles that arise on the floor of the epicranium nearly 0.1 mm. behind the bases of the tentoria and are inserted on the struts near the origin of the protractors of the maxillae. These muscles were not recognizable in the specimen from which figures on plate 13 were drawn, but have been inserted in two instances (figs. 10 and 11) from another series of sections.

The head of the Anopheles mosquito is relatively higher and broader in the epicranial region than the head of Culex and the pre-ocular region slopes downward. This makes the muscles run forward at different angles from those in Culex and sections of the two forms appear somewhat unlike, although, with a single exception, the same muscles are present in both. The muscles of the mouthparts and head, outside of those supplying the alimentary canal, differ from the muscles of Culex as follows. The retractors of the maxillae arise more laterally and fully 30 μ caudad from the bases of the tentoria, so that their origin is wholly from the walls of the head and not partly epicranial and partly tentorial. The posterior or apodeme ends of the protractors of the maxillae also, lie farther back and the upper or tentorial ends are in the same level as the double retractor muscle. Hence both protractor maxillae and double retractor muscles may be present in one section, which is not the case with Culex where the origin of the protractors is distinctly caudad from the origin of the double retractors (pl. 13, figs. 7, 15). The subocular muscles are much larger, and arising farther back in the head, they are less likely to be mistaken for fibers of the retractors of the maxillae. They are inserted on the tentoria immediately caudad of the origin of the double retractor muscles, near the insertion of a pair of minute transverse muscles, not represented in Culex, which arise on the walls of the epicranium dorsal to the origin of the anteriormost lateral dilator of the esophagus.

The fore gut. — The stomodaeal portion of the alimentary tract of insects is subject to great variations with respect to the number and character of the regions that are differentiated in it. It may well be considered doubtful if homologies between regions can legitimately be sought beyond the limits of any one order. Hence a nomenclature for the various parts need only be self-consistent within a single order and may properly be subject to individual preferences. The stomodaeum of the imagoes of the Diptera offers especial obstacles to the establishment of a system of names that shall meet all conditions, for there is a considerable range of variation within the group. For example, in Musca (pl. 14, fig. 16) the labral or proboscis canal (*pc*) is succeeded by an intracephalic subclypeal pump (*ph*) which shows distinct anterior and posterior regions. Then the esophagus (*oes*) commences and hence extends through the circumesophageal nerve-collar or "brain." In other

flies with a similar succession of proboscis canal, subclypeal pump, and extensive esophagus, the differentiation of the subclypeal tube into two regions appears to be wanting. In contrast to the arrangements in these flies, the Tipulidae (pl. 14, fig. 18) have a chitinous "pump" in the region of the brain (*pump*) and the esophagus is restricted to the extreme rear of the head. The Culicidae (pl. 14, fig. 17) resemble this last mentioned family with the exception that the "pump" is dilated behind the nerve-collar instead of being of nearly uniform diameter throughout its length. The Simuliidae possess a "pump" which is not markedly dilated at any point, but it is distinctly divided into a preneural and a postneural portion. This subdivision foreshadows the arrangement found in the Asilidae and Tabanidae (pl. 14, fig. 19). Here the postneural part of the "pump" is vestigial while the preneural part is strongly developed. If a nomenclature is to be satisfactory for all cases it clearly must take into account three differentiated regions of the stomodaeum, in addition to the unspecialized esophagus: the proboscis canal of the labrum (*pc*), the subclypeal tube (*ph*), and the more posterior chitinized "pump." Of these the subclypeal tube and the pump may be subdivided. Two additional factors must be considered. The subclypeal tube appears to be an essentially homologous structure throughout the group of the flies and the pump probably corresponds to the anterior end of the elongate esophagus of those flies where only a subclypeal tube (*ph*) is differentiated, *e. g.*, Muscidae. A system of names which groups the subclypeal canal and pump under a single expression is therefore inadvisable, as for example Christophers' and Annett and Dutton's accounts where these regions collectively form the "pharynx" or Hurst's description in which the terms "buccal cavity" and "pharynx" are used indifferently for all the specialized intracephalic stomodaeum.

Two systems of nomenclature for the Dipteran stomodaeum which are free from the objections cited, exist. The older seems to have come into being by simple extension of the names given to the parts in Musca, *i. e.*, "pharynx" for the subclypeal tube, and "esophagus" for all the remaining fore gut. Thus Meinert ('81) calls the pump of Tabanus and Asilus "pars prior oesophagi" or "pars tumida oesophagi." With Culex or Tipula this region is simply "oesophagus." Dimmock ('81) with respect to the parts in Culex, the most

complicated type of Dipteran alimentary canal that he studied, refers to the pump as "oesophageal bulb" and to the subclypeal canal as "pharynx." On the other hand, Nuttall and Shipley (:01–:03) in their careful study of Anopheles term the subclypeal canal "buccal cavity" and the pump "pharynx." The older of these nomenclatures has decided advantages over the newer system used by Nuttall and Shipley in that it recognizes the probable equivalence between the pump and the anterior end of the "esophagus" of such a fly as Musca, and in that it gives the expression pharynx — which is generally employed in insect morphology to indicate the first differentiated intracephalic region of the stomodaeum — to the constantly present subclypeal canal rather than to the inconstant pump. It also leaves the term buccal cavity vacant and available for any subregion of the subclypeal canal which it may seem best to delimit.

A study of the larvae of the Diptera in the above connection offers no assistance, but rather complicates the problem. A majority of Dipterous larvae have a fore gut that is practically undifferentiated throughout its cephalic extent. In other forms, well marked regions are present. But these are not always comparable, even in closely allied genera, *e. g.*, Culex and Corethra. Further, the larval regions may or may not coincide with the regions of the imaginal tract. The wriggler of Culex has a buccal cavity and a pharynx, the latter being imperfectly distinguished from the esophagus below and at the sides. But the larval buccal cavity and pharynx both go to form the subclypeal canal of the imago and the pump of the latter stage is derived from the anterior end of the esophagus of the larva. Such peculiarities find their explanation in the extremely adaptive character of the Dipterous larva, but this in turn makes it unwise to lay stress on larval relations, in an attempt to obtain a system of names for the imaginal parts.

Employing the nomenclature just chosen, the stomodaeal portion of the alimentary canal of the mosquito shows successively: the labral or proboscis canal, the subclypeal tube or pharynx, the pump or antlia, and an esophagus which extends through the occipital foramen into the thorax. The midgut is differentiated into cardia and stomach or mid-intestine. The hind gut is modified to form an ileo-colon and a rectum. Valves are developed at the union of pharynx and antlia, pharyngeo-esophageal valve, at the posterior end of the antlia, at the junction of esophagus and cardia, eso-

phageal valve, and at the point where the stomach and ileo-colon come together.

According to Dimmock ('81) both labrum and hypopharynx take part in the formation of the proboscis canal, the latter stylet forming the floor. Kräpelin ('82) on the other hand, considers that this canal is wholly labral in origin. It was not possible to decide between these views. The shelf formed by the produced lower internal angles of the labrum (pl. 16, fig. 46–47) favors Kräpelin's view, but in this case the delicate character of these plates would seem to require that the hypopharynx should be drawn up against them during blood sucking and so indirectly complete the proboscis canal ventrally.

Since the anterior wall of the clypeus is forward of the bases of the mouthparts generally, the labrum meets the head some distance in front of the point where the mandibles, maxillae, hypopharynx, and labium are inserted. In this region the section of the proboscis canal is that of an arch, and the hypopharynx unquestionably supplies the flattened floor (pl. 13, fig. 3). Caudad of the bases of the mouthparts (pl. 13, fig. 4) the canal may be considered as intracephalic and as pharynx. At this point the thick chitin of the side walls of the canal thins abruptly and in material cleared with caustic the proboscis canal appears to terminate with a spur on either side. There is no real point of demarcation, however, between the proboscis canal and the pharynx as I have limited them, except the completion of the tube as the mouthparts join the head and the formation of these seeming spurs. The chitin of the floor of the canal is already thin and so harmonizes with the thinned walls. On the roof of the canal the heavy chitin extends for a considerable space into the head, thinning out gradually from the sides toward the midline, and so forming a tongue of heavier chitin amid the weaker chitin. Nuttall and Shipley's description of this structure, anterior hard palate in Anopheles as "somewhat in the form of a trowel" is equally vivid for Culex, since its arch is steeper than the arch of the pharynx roof generally (pl. 13, fig. 5). Just before this palate terminates, its surface is roughened by a few minute conical spines. The proboscis canal receives immediately anterior to the "spurs" at its proximal end, a pair of muscles from the alae of the clypeus. These are the "epipharyngeal muscles" (Annett and Dutton, :01) and the region of their insertion closely corresponds to that

occupied in the larva by an epipharynx-like structure. Meinert ('81) figures for Culex muscles joining the alae of the clypeus to the roof of the box. I have not been able to find these in three species of Culex at my disposal, and they are not present in *Anopheles punctipennis*.

The pharynx extends from the union of the mouthparts with the head to the anterior end of the esophageal antlia. It is developed as a pumping organ and the character of its walls and the form of its cross section vary in different levels. At first, in the region of the anterior hard palate, the floor and walls have a thin intima throughout and this steadily involves more and more of the roof of the canal as the anterior hard palate narrows. At the same time the floor of the pharynx becomes curved, so that by the time the trowel-shaped hard palate has vanished, the pharynx consists of a curved ventro-lateral plate and a flattened dorsal plate, the two meeting in high dorso-lateral angles (pl. 13, fig. 6). The section of the tube is either crescentic or that of an inverted arch, according to the position of the dorsal plate as it curves down into the lumen or is drawn upward by muscular action. For a space after the hard palate vanishes, both walls and roof remain thin. Then the dorsal plate becomes uniformly thicker. Finally, thinning again, it forms the pharyngeo-esophageal valve at the entrance to the antlia. Hence the dorsal plate or roof of the pharynx is differentiated into four regions: an area of thin chitin with a median tongue of thicker chitin, anterior hard palate; a region with uniformly thin chitinous intima, soft palate; a region with uniformly denser intima, posterior hard palate; and a narrow area of thin chitin forming a valve. The valve and posterior hard palate regions are derived from the "pharynx" of the larva. The remainder of the pharynx and the proximal part of the proboscis canal are formed from the "buccal cavity" of this earlier stage.

The chitinous intima of the floor and side wall of the pharynx is uniformly thin except in the region of the posterior hard palate. Here, beginning first along the border of the dorso-lateral angles, an area of thicker chitin forms on either hand and widens to involve all the wall of the canal for a space. Then narrowing again, these areas terminate with stout spurs which project past the anterior end of the antlia. At the point where they are most extensive, they meet across the floor of the pharynx and in the female insect a

delicate crest projects downward from this traverse. The male Culex has the same arrangement of thickened areas but lacks the crest. The development of these thickened areas in the walls of the pharynx near its union with the antlia must make the ventro-lateral plate rigid at this point. The antlia has also at its anterior end rather unyielding walls. Hence the thin dorsal plate beyond the posterior hard palate forms an efficient pharyngeo-esophageal valve, dipping into the lumen of the canal through elasticity and being withdrawn by muscles.

At its anterior end the pharynx for a space is firmly bound to the walls of the head by an ascending chitinous plate on either side. These plates are continuous with the cuticle of the head and the intima lining the pharynx, and represent intracephalic continuations of the plates formed by the union of the genae with the clypeus (pl. 13, fig. 3–5). The plates soon degenerate into low crests along the dorso-lateral angles of the pharynx and fade out.

At its hinder end the pharynx is held in place by two pairs of muscles. The shorter of these, the lateral pharyngeal muscles, run outward from the external face of the spurs at the rear of the pharynx to the tentoria. The others, the ascending pharyngeal muscles, pass from the internal face of the spurs to the vertex of the head.

The pharynx as a pumping mechanism is constructed on the same principle as the salivary pump or antlia. The lumen is diminished by the inspringing of the chitinous dorsal plate, which is withdrawn again by the action of muscles. The muscles which lift the roof of the pharynx in this pumping action may be called the elevators of the palate (Nuttall and Shipley, :01–:03). When compared with the homologous muscles of many flies these muscles appear relatively weak. They are considerably specialized, however, as there are five distinct pairs, instead of a single mass or at most a larger anterior and a smaller posterior section. When this latter differentiation occurs the posterior section is called the protractor of the pharynx (Meinert, '81). Possibly it finds its equivalent in the fifth pair of the Culicid muscles. Of the five pairs, the anteriormost insert on the rear of the anterior hard palate region, the next on the soft palate, the three posterior pairs on the hard palate. The pharyngeo-esophageal valve is elevated by a pair of valvular muscles from the frons. These lie caudad from the buccal ganglion. The valvular, ascending pharyngeal, and lateral pharyngeal muscles are described

by Nuttall and Shipley, but are not named. The elevators of the palate are the "musculi antliae pharyngis" (Meinert, '81), the "pharyngeal muscles" (Annett and Dutton, : 01; Dimmock, '81, in part), and the "protrusor muscles of the labrum" (Giles). The last identification is based on the figures. The accompanying description is obscure.

The pharynx serves as origin for two pairs of muscles. Near its anterior end the maxillary muscles arise and near the posterior end the hypopharyngeal muscles. These latter operate the salivary pump. With the female of Culex they have an extensive origin from the walls of the pharynx between the ventrally projecting crest already described and the neighborhood of the third pair of elevators of the palate (pl. 12, fig. 1, *hyp m*). They arise in part also from the lateral borders of the crest, but not from its median surface. In the male the smaller muscles have a limited origin in the level of the third pair of elevators of the palate. No muscle with the position assigned by Giles to his "muscle opening the salivary valve" could be found in either Culex or Anopheles and the account of the salivary gland given by him is misleading in other respects. The hypopharyngeal muscles correspond to Giles' "muscles closing the salivary valve," to Meinert's "retractores receptaculi," and to Annett and Dutton's "muscle to the salivary receptacle." Nuttall and Shipley describe these muscles but do not name them.

The structure of the pharynx described for Culex is closely paralleled by that found in the malarial mosquito. There is the same succession of anterior hard, soft, and posterior hard palates and valve, but for *Anopheles maculipennis* as described by Nuttall and Shipley, the structures on the intima in the region of the tip of the anterior hard palate are more complicated than they are in Culex. Annett and Dutton describe for *A. costalis* a complex arrangement of hair-like processes on the ventral plate of the pharynx below the pharyngeo-esophageal valve. Nuttall and Shipley record that they failed to find such structures in the species of Anopheles that they studied, *A. maculipennis*, and I do not find them in *A. punctipennis*. The bracing of the pharynx to the walls of the head anteriorly and the formation of heavily chitinized areas and terminal spurs posteriorly are similar in both genera and in Anopheles also the ventral crest is developed as a partial origin for the hypopharyngeal mus-

cles. It would appear that the pharynx of Anopheles has somewhat more sharply marked angles than the pharynx of Culex and may therefore be a more effectual pump. The muscles are the same as in Culex: hypopharyngeals from the walls and crest of the pharynx, five pairs of elevators of the palate with the same relations to the soft and posterior hard palates, epipharyngeals from the alae of the clypeus, lateral pharyngeals, ascending pharyngeals, and valvulars. The ascending pharyngeals arise from the median internal crest alone and not from crest and vertex of the head as is the case with Culex.

The antlia of the female mosquito is pyriform with the bulb behind the nerve-collar. The chitinous intima which lines this part of the alimentary canal is so modified that it is convenient to speak as if it were composed of three racquet-shaped plates, one dorsal, the others ventro-lateral in position.

The borders of the plates are reflected and a thin band of chitin is included between each adjacent pair of plates. The plates can spring inward until they almost obliterate the lumen of the canal (pl. 13, fig. 12) or be drawn back by muscles until the lumen of the bulb has a nearly circular section. As the plates terminate posteriorly they are clothed by a dense coat of fine bristles and this development continues for 10 μ or more on the thin intima of the esophagus. The postneural bulb is the active part of the pump. Here the dorsal plate receives two large dorsal dilator muscles from the vertex of the head. These muscles are compressed and in an average female of *Culex stimulans* their greatest diameter was 60 μ, the lesser diameter 31 μ. In a male of the same size the corresponding diameters were 60 μ and 15 μ. These muscles correspond to the "musculi superiores antliae" (Meinert, '81) and to the "superior pumping muscles" (Christophers, :01), "post dorsal dilators" (Nuttall and Shipley, :01–:03). Either lateral plate receives five lateral dilator muscles from the sides of the head. These muscles trend forward and upward to their insertions and are compressed. In an average female of *C. stimulans* the greatest diameter of the first to the most posterior muscle was 54, 56, 72, 54, and 44 μ respectively and the lesser diameter 27, 20, 37, 18, and 20 μ. The total cross section of the female's muscles is nearly twice that of the muscles of the male. The lateral dilators have been described as "musculi inferiores antliae" (Meinert, '81), "lateral pumping mus-

cles" (Christophers, :01), "muscles of the pumping organ" (Annett and Dutton, :01), "dilator muscles" (Giles, :02). Dimmock figures and refers to the lateral and dorsal dilator muscles but does not name them. In the anterior, preneural, part of the pump the ventral uniting strip between the ventro-lateral plates — always broader than the two dorso-lateral strips — becomes wide and flat, so that the antlia in this region is four-sided (pl. 13, fig. 8). This must diminish the movement of the walls and dorsal plate. At this point the dorsal plate receives a vestigial dorsal dilator muscle (*ant dil*). In Anopheles, where the activity of this part of the pump is less diminished, two dilator muscles reach the dorsal plate, "anterior dorsal dilators" (Nuttall and Shipley, :01–:03).

The epithelium of the proboscis canal, pharynx, and antlia is inconspicuous. It is flattened over the proboscis canal and antlia more than over the pharynx. The intrinsic muscle coats are not evident, except over the hinder end of the antlia where a powerful sphincter muscle is developed (pl. 12, fig. 2, *sph m*).

The male of Culex has a more attenuated antlia with a relatively smaller bulbous portion than the female. The total capacity is less than that of the female's antlia even when the latter insect is represented by a smaller specimen. Computed by Cote's rule, the largest male antlia found in *C. stimulans* had a capacity of approximately 0.0008 cu. mm. The smallest female antlia of the same species measured 0.002 cu. mm., and the largest 0.004 cu. mm. The time taken by a mosquito of this species to draw up its meal of blood depends on the nature of the spot pierced, averaging according to my observations about one minute for a light and nearly half as long again for a heavy meal. But under especially favorable conditions the lesser meal can be taken in 50 seconds, the greater in 65 seconds. Since a heavy meal consists of nearly 4.5 cu. mm. of blood, a very rapid action of the antlia would seem to be required, especially if this pump empties itself at each stroke. More probably, however, it acts to maintain a continuous rather than an intermittent flow.

The antlia of Anopheles corresponds closely to that of Culex in structure. The most important difference is the greater functional activity of the anterior or preneural part as a pumping organ with an accompanying development of the anterior dorsal dilator muscles. As a result, the antlia of Anopheles is more uniformly cylin-

drical than the antlia of Culex. This point of difference is of interest in connection with the varied specialization of the antliae in the Diptera. On a basis of their pumping mechanisms the group can be separated into two main groups, which may be termed monantlial and diantlial. The former division includes the Muscidae (pl. 14, fig. 16), the Syrphidae, and other families the members of which possess only the pharyngeal pump. The diantlial group have both a pharyngeal pump and an antlia. Among these flies several forms of antlia are found. For example, Culex (pl. 14, fig. 17) and Anopheles have an antlia which is best developed behind the "brain," *i. e.*, it may be described as postneural in type. As already noted, the pump of Anopheles is less markedly postneural than that of Culex, approaching what may be called the amphineural type, where it is nearly cylindrical throughout. The Tipulidae are perhaps the best example of this type of antlia (pl. 14, fig. 18, *pump*). Simulium, while amphineural with respect to the form of its antlia, has this region differentiated into distinct pre- and postneural sections. The antlia of the Tabanidae (pl. 14, fig. 19) and the Asilidae is not only subdivided as in Simulium, but the preneural part alone is functional, the post-neural section being rudimentary. This type may be called preneural.

The tracheation of the head is interesting with respect to the supply to certain parts of the alimentary canal and muscles. Thus the extensive tracheal supply to the elevators of the palate shows that these muscles are of considerable use, and that the pharynx, although overshadowed by the great esophageal pump, is yet by no means unimportant as a suctorial bulb. The thoracic portion of the alimentary canal is paralleled on either side by a tracheal trunk. From either trunk two tracheae are given off into the head, the external and internal tracheae (pl. 13, fig. 12). These lie close to each other until they have passed the dilator muscles and then part company. The external trachea ascends into the cleft between the optic ganglion and the "brain" (pl. 13, fig. 10), supplies these nervous masses and the protractor muscle of the maxilla, and then breaks up into branches some of which run in the mesial plane of the clypeus to supply the labral muscle and the elevators of the palate. The internal trachea follows the ascending line of the tentorium and its terminal twigs reach the head of the strut. But before this point is attained, the trachea has spent itself in two large branches. The

first to arise, the labial trachea (*li tra*), runs forward between the double retractor and retractor of the maxilla muscles and enters the labium. It gives branches to the double retractor, the retractor of the maxilla, the salivary pump, and probably to the mouthparts generally. One prominent tracheole follows the double retractor muscle, so that this muscle has an extensive tracheal supply. The second branch of the internal trachea (pl. 13, fig. 6–9) trends sharply upward and divides to supply on the one hand the maxillary palpus and on the other the lateral pharyngeal and antennal muscles and the elevators of the palate, which thus receive a double tracheal supply. A median tracheole reaches the labral muscle at its origin.

The esophagus is mainly thoracic in the female Culex and almost wholly so in the male, owing to the more truncate head which leaves less space beyond the antlia. The esophagus is a slender canal with thin walls, lined with a delicate intima which is smooth except for the area of bristles at the anterior end. The walls are composed of a single layer of flattened epithelial cells, the boundaries of which can hardly be distinguished in sections. The usual muscle coats are present, but poorly developed. Near the posterior end of the esophagus three diverticula arise, two from the dorso-lateral and one from the ventral wall of the gut (pl. 14, fig. 20, *f res*). Then the esophagus terminates with the esophageal valve, a shallow curtain which dips into the first region of the midgut, the cardia. Within this valve the otherwise insignificant circularis muscle coat is specialized to form an annular muscle. The valve appears to be without an external blood sinus and its walls have an epithelium similar to that of the esophagus. Unless the cardia is greatly distended, the point where the epithelium of the esophagus ceases is very noticeable at the shoulder of the cardia near the termination of the reflected face of the valve (pl. 16, fig. 41).

The dorsal esophageal diverticula are small and lie close to the dorso-lateral walls of the prothorax. The ventral pouch is large and may extend into the abdomen. It does not appear to be as large relatively as the corresponding pouch in Anopheles. Usually all three sacs are filled with bubbles of air, and I have never found anything else in them. Nuttall and Shipley (:01–:03), however, have made a careful study of the possible functions of these pouches in Culex and seem to have conclusively demonstrated that they serve

as food reservoirs. Other investigators record the detection of blood in the sacs of the mosquito and the similar pouches developed in other flies occasionally contain food. In view of these facts there seems to be no good reason for denying that these diverticula serve as storage places for food. The name "food reservoirs" (Nuttall and Shipley, : 01–: 03) or "esophageal diverticula" (Granpré and Charmoy, : 00) should replace the older and misleading terms "aspiratory vesicles," "suctorial vesicles," etc.

When one of these diverticula is extracted and is examined under a microscope, the only structure noted at first is an irregular and varying mesh of delicate striae. More careful study makes it clear that these "striae" are wrinkles or folds of the delicate intima that lines the pouch, varying in size and position with the torsion or tension of the particular part under observation. By staining the fresh tissue with Bismark brown, distinct muscle fibers become visible and the nuclei of the epithelium appear (pl. 16, fig. 42). With a $\frac{1}{12}$ oil-immersion lens the epithelium itself can be distinguished in places as a granular cloud. Whether the muscle bands have as regular a distribution with Culex as the similar bands described by Nuttall and Shipley on the ventral sac of Anopheles, was not determined. The "striae" sometimes pass across a muscle without alteration, but usually, of course, they are more numerous along the line of the muscle, interlacing and radiating in groups from its borders. Under a low-power lens this gives them a strong resemblance to muscular fibrillae. The appearance vanishes when a higher magnification is used, but should be noted, since, with some reagents — *e. g.*, methylin blue — the color fills the "striae," seemingly staining them. If a pouch is torn the excessively wrinkled intima gives a fibrous appearance to the fragments. This is probably the basis for Giles' assertion that these organs are composed of finely branched tracheae. "The fibers are neither more or less than extremely elastic and distensible tracheae, which swell out into bubble-containing dilatations. . . . . Apart from a few loose connective elements the sacs consist of nothing else than these curiously modified tracheae." In connection with this statement with respect to structures that are obvious diverticula from the esophagus and have a less extensive tracheal supply than any other part of the alimentary canal, except possibly the pharynx and antlia, Giles also holds that there are two ventral sacs, that there is no organic connection between the esophagus and

the sacs, and that the pouches have an aerostatic function. Nuttall and Shipley (:01–:03) have thoroughly exposed the inaccuracy of this account of the sacs of Anopheles. It would be equally inapplicable to Culex. The two genera show no essential differences with respect to the structure of the food reservoirs.

Salivary glands.— The epithelium of the salivary duct is thin but columnar and the duct has a trachea-like aspect owing to annular thickenings of its intima. It forks within the head and in the thorax each branch supplies a tripartite gland. The duct within each of the three acini of the gland is (*Culex stimulans*) of uniform diameter, has a delicate smooth intima, and is traceable to the apex of the acinus where it ends blindly. The acini are elongate and as their first describer Macloskie ('88) and later writers have noted, the central and lateral divisions are unlike in appearance. Macloskie gives no evidence to support his suggestion that the central acinus secretes the poisonous element of the saliva. This acinus (pl. 14, fig. 23, *ca*) is slender, cylindrical, and its nuclei are prominent, surrounded by granular cell contents. In sections the larger part of each cell is filled with secretion which, as precipitated by the reagents, stains lightly with haematoxylin and is coarsely granular. The nuclei are pushed over against the basement membrane. The lateral acini apically are of the same diameter as the central acinus, but their bases are distended. Their cells are filled with a transparent secretion of high refractive index. Toward the base of the gland nearly every cell contains a huge ovoid vacuole filled with the secretion which forces the nucleus against the basement membrane. Sections show clear spaces where these vacuoles were situated. Nearer the apices of the acini the vacuoles are smaller and less numerous.

The differences in the appearance of the lateral acini and the central acinus are due to the different substances secreted and stored in the cells. During the later pupa stage the distinctions are wanting and all parts of the gland resemble the central acinus of the imago as viewed by transmitted light. Sections, however, show no secretion in the cells. The differences make their appearance a short time before the imago emerges.

The midgut.— The part of the midgut which receives the esophageal valve (pl. 14, fig. 20) is best called the cardia. As with most other flies, the region is not definitely marked off from the

stomach in either Culex or Anopheles. Sections show only a gradually increasing affinity for haematoxylin on the part of the cells as the esophageal valve is approached. In shape and other characters the cells resemble those of the stomach generally and there is no alteration in the muscle coats. The stomach extends into the seventh abdominal segment and is the longest single region of the alimentary canal. Its thoracic end is a narrow tube, but the abdominal part is wider and capable of great distension. Here is stored the meal of blood while it is being digested. The wall of the stomach has an epithelium composed of small cubical cells with oval nuclei and granular cytoplasm (pl. 14, fig. 21, *st*). The free border of the cells is more transparent than the remaining area. Probably this corresponds to the "striated border" described by Christophers (:01) for Anopheles. The margins of the cells make a very sharp line in sections, but I did not succeed in demonstrating a cuticle. In the freshly removed stomach the nuclei are not visible and the cytoplasm appears filled with refringent granules. Over the surface delicate circular and longitudinal muscles pass in an irregular network which cuts the surface into more or less rectangular areas. The epithelium often protrudes between the muscles forming "islands" of one or more cells. The stomach narrows suddenly at the posterior end and a low valve is formed. The tracheal supply is extensive and the interlacing vessels serve to retain the canal in position.

The physiological dissimilarity between the stomachs of Anopheles and Culex in relation to the malarial parasite may possibly be accompanied by visible histological differences, although none have so far been described. Conclusive proof awaits the elaborate process of removing stomachs from mosquitoes of both genera when in the same physiological state, and passing them through all the reagents simultaneously. I have not been able to obtain a sufficient number of Anopheles to do this.

The hind gut.— The anterior end of the first region of the hind gut, the ileo-colon, is modified to form a low valve adjacent to the valve (pl. 14, fig. 21) which terminates the midgut. The Malpighian tubules open into the circular cleft between these two annular valves. There are five Malpighian tubules, an unusual number among the flies. They extend forward for a space parallel to the stomach and then recurve, their tips reaching into the last joint of

the abdomen. In fresh material under transmitted light the cytoplasm is steel gray in color, the nuclei are transparent, and the cells are filled with refringent granules. Sections show a definite structureless border along the free edges of the cells. This stains deeply with "orange G" but I am not certain whether it is to be regarded as a cuticle.

The ileo-colon is a canal of small diameter and its walls are thin. The cytoplasm of the epithelial cells as seen in sections is often vacuolated, especially toward the base of the cells. A thin, distinct, cuticular lining is visible, and for a short space immediately behind the entrance of the Malpighian tubules this is roughened by bristle-like chitinous papillae which point caudad (pl. 14, fig. 21, *ilc*). This hirsute belt cannot be regarded as characterizing a "region" in the gut of the imago and the area does not correspond to any distinct region in the hind gut of the larva. The longitudinal and circular muscles of the ileo-colon are fairly well developed and like the stomach this part of the alimentary canal has an extensive tracheal supply.

Posteriorly, the ileo-colon passes imperceptibly into the rectum. The depth of the epithelial cells of the rectum is variable and the muscle coats are less developed than in the ileo-colon. There are six rectal papillae, each consisting of a cone of large epithelial cells arranged about a common axis. The tracheal supply to the rectum is generous, especially to the papillae. Tracheae derived from the main longitudinal trunks that follow the alimentary canal on either side run to each papilla, emit branches that course over the base of the cone and adjacent walls of the rectum, and then one or more branches enter the axis of the papilla. These axial tracheae ascend to the apex of the cone and divide, their branches curving back in a somewhat tortuous course among the component cells.

The Larva.

The larger and broader head and the elongate respiratory siphon on the dorsum of the eighth joint of the abdomen are perhaps the most obvious of the external differences that distinguish the wrigglers of Culex from those of Anopheles. Otherwise the ground plan is similar: the three thoracic segments are consolidated into a single

mass and there are nine abdominal joints, of which the eighth bears the respiratory siphon and the ninth four anal valves and a ventral keel of setae. Under the scope of this paper the head alone requires detailed description.

The head of the Culex wriggler (pl. 15, fig. 29–32) is flattened in the dorso-ventral plane. Forward of the antennae it narrows. Behind them its cross section would resemble that of a watch, a flattened oval. The dorsal surface is the more convex, descending rapidly in the rear, more gently at the sides, and with a comparatively steep slope forward from the antennae. The anterior margin of the head is bounded by a border line of thickened chitin (*bord l*) beyond which a shelf-like fold projects. The shelf bears two simple setae. The investing cuticle of the top of the head is strong and is reinforced by two thicker scythe-shaped areas (*sca*) which extend backward from the antennae. At pupation the cuticle splits along the inner margin of either area to the occipital foramen. On the ventral side of the head the transverse line (*tr l*) separates the pre- from the post-antennal region. This boundary consists of a narrow-linear band of dark, thickened chitin laterally and a low transverse fold mesially. Heavy cuticle extends over the post-antennal ventral region of the head and is traversed by two narrow-linear "lines" of dark, thickened chitin which pass from the transverse line to the border of the occipital foramen. These divergent lines support the ventral ends of the tentoria, the black, triangular, mental sclerite, and furnish a point of origin for the depressors of the antenna (*ant m*) and other muscles. At pupation the ventral head cuticle splits in the midline from the occipital foramen to the transverse line.

The relations of the pre-antennal region of the head are hard to describe. As noted, the dorsal surface is convex and heavily chitinized. The ventral face slopes sharply inward and downward toward the entrance to the pharynx, a point almost in the center of the head. Thus the pre-antennal region is in reality a broad rostrum which overhangs the mouthparts, situated near the transverse line below, slightly forward of the entrance of the pharynx (pl. 14, fig. 26). Its cross section would be the segment of a circle, the arc being represented by the convex dorsal surface. In the mid-ventral line, about halfway between the anterior shelf-like fold and the entrance of the pharynx, a crest is formed. This bears four

stout setae and is flanked by setose areas. Here the thin chitin characteristic of the ventral face of the rostrum generally, is strengthened by a triangular sclerite. I regard this structure as an epipharynx. It receives a pair of slender muscles (Raschke, '87) which arise on the top of the head and probably function as retractors.

The border line and shelf-like fold already described, mark the boundary between the heavier chitin of the dorsal and the thinner chitin of the ventral face of the rostrum, above and in front. But on either side, near the antennae, the thicker chitin involves part of the ventral face of the rostrum. These inflected areas of heavy chitin I call the black-spot areas, because each bears a conspicuous patch of pigment (*blks*). From either area a narrow-linear "line" of heavier chitin traverses the ventral face of the rostrum to strengthen the sclerite of the epipharynx. In the bay of thin cuticle bounded in front by the anterior shelf and border line, and posteriorly by the black-spot areas, lie the small, median palatum (*pal*) and the larger, lateral flabellae (*fl*). These are protuberances, densely clothed with fine hairs, the flabellae having in addition a peculiar arrangement of long yellow setae. Black-pigmented apodemes (pl. 15, fig. 31) that are continuous externally with the black-spot areas enter each flabella and the two flabellae are united by a transverse rod. To the apodemes the flabellal muscles (*retr fl*) are attached, two for each flabella, an inner and an outer, both retractor in function and acting simultaneously. When these muscles contract the seta-bearing area of the flabella is depressed and the setae come together in a brush whose tip points caudad. On their relaxation the flabellae protrude beyond the front of the head and the setae stand out in great yellow fans. The median prominence or palatum passively follows the movements of the flabellae, which are strictly synchronous, as far as I have observed.

The mouthparts.— The mouthparts (pl. 15, fig. 29, 32) of a Culex wriggler consist of huge maxillae, moderate sized, toothed mandibles and sclerites which represent labium and hypopharynx. The maxillae conceal the greater part of the under surface of the rostrum. The palp is minute. These appendages are not joined to the head by definite articulations as are the mandibles, and do not move as freely. Within the epipharynx above, mandibles, maxillae at the

sides, and transverse line below, lies a funnel-shaped cavity leading to the pharynx. Into this space the tips of the flabellal setae dip when those organs are depressed. It may be called the buccal cavity, and within the transverse line four structures are successively differentiated from its floor: a delicate, hair-fringed crest, a black, triangular mental sclerite (*tr*), a complicated saddle-shaped sclerite with a median crest and lateral toothed spurs (*li*), and confluent with this last, an arch of heavy chitin which is pierced by the orifice of the salivary duct (*hyp*). The mental sclerite is braced to the divergent lines at its lower angles. The arch sclerite, and indirectly through it the saddle-shaped sclerite, are strengthened by a narrow-linear "line" of heavy chitin (pl. 15, fig. 31, *htr*) which crosses the thin chitin of the buccal cavity from the black-spot area of either side. These hypopharyngeal traverses give support also to the walls of the pharynx by short apodemes.

The mental sclerite was called "under lip" by Meinert ('86) and corresponds to the structures figured by Miall and Hammond for larvae of Chironomus, ('92, :00), Miall ('93) for Dicranota, and Miall and Walker ('95) for Pericoma as "submentum." Raschke identified the fold that I have termed the transverse line with the mentum, "kinn." For Miall, the sclerites which correspond to the saddle-shaped sclerite of Culex are "mentum." With Culex, however, this sclerite sheathes the bud which forms the labium of the adult and is to be regarded as the larval labium. The mental sclerite would seem to be either a mentum or a submentum, as its hypodermis during the metamorphosis passes into the floor of the head (pl. 15, figs. 34, 36, *fold*).

The mandibles have a powerful musculature. Each receives a converger muscle on the lower internal angle and a divaricator on the lower external angle. These muscles arise by triple heads on the walls of the epicranium. Each maxilla has two muscles. One consists of two parallel bands and arises near the origins of the mandibular muscles (*dep max*), the other is single and arises from the divergent line (*retr max*). Both insert at the middle of the base of the maxilla. The action of these muscles was determined with difficulty, but by watching slow contractions in a dying larva it was found that the double band pulled the maxilla caudad and a little outward (ventrad) while the single muscle pulled the maxilla caudad and inward (dorso-mesad). Hence the double muscle may

well be called the depressor of the maxilla, the single muscle the retractor of the maxilla. The labium is supplied by a pair of muscles running from the divergent lines to the hinder angles of the sclerite. They are depressor in action. Under the hypopharyngeal sclerite are a few scattered muscle fibers.

The fore gut.— The fore gut of the Culex larva is divided into buccal cavity, pharynx, and esophagus. The buccal cavity has already been described. Its epithelium is columnar and behind the epipharynx above and the hypopharynx below there is a considerable area of undifferentiated intima (pl. 15, fig. 32, *bc*). The pharynx is sharply marked off from the buccal cavity by a fine line of denser chitin and its flattened epithelium serves as a further distinction. The pharyngeo-buccal and pharyngeo-esophageal openings are not in line, since the esophagus leaves the pharynx rather from the floor, and in longitudinal sections the rear of the pharynx often overhangs the esophagus like a blind pouch (pl. 15, fig. 32). This appearance is an artifact, due to the contraction of the walls of the esophagus when the animal is killed. Actually, pharynx and esophagus are not sharply delimited. The general appearance when dissected out of the head, is as if the esophagus expanded to form a cup with high-arched sides (pl. 15, fig. 35) open widely in front where the walls pass to the buccal cavity and closed above by a dorsal plate. The arching borders where walls and roof meet may be termed the crests of the pharynx. They are approximated at the extreme rear of the pharynx (pl. 15, figs. 30, 33) and as they sweep forward in the high curve and descend again toward the buccal cavity, they diverge. The dorsal plate or roof of the pharynx therefore is narrowed posteriorly. When at rest the angle between the posterior ends of the crests measures about 60 degrees. But the side walls of the pharynx are mobile and may approach or spread apart from one another. The angle between them consequently varies, and the dorsal plate must accommodate itself to changes in the width of the space between the crests. This is accomplished by folding the plate inward along its median line. When the pharynx is dilated, the dorsal plate is almost plane, but when the walls of the pharynx approach each other strongly, the plate folds in until it nearly touches the floor beneath. The folding is most marked posteriorly and becomes progressively weaker toward the anterior end of the pharynx, where a transverse crescentic sclerite

is developed in the dorsal plate and very possibly serves as a check (*cres*).

The pharynx has an elaborate musculature. The two halves of the dorsal plate are united by transverse or oblique bands (*dor ph*) which attach to a longitudinal sclerite developed on either side of the median fold. A pair of diagonal muscles (pl. 15, figs. 30, 33, *diag*) reach the pharyngeal crests near their posterior ends, from origins on the roof of the head, in each case on the side opposite to that of the insertion. At the summit of their curve the crests receive lateral muscles (*lat m*) from the scythe-shaped areas on the walls of the head, while nearer the border of the buccal cavity, several lesser lateral muscles (*less lat*) reach the dorso-lateral walls. At their approximated posterior ends the crests are bound to the epicranium by stout muscles, the retractors of the pharynx (pl. 15, figs. 30, 32). The hinder parts of the dorsal plate furnish insertion for two elevators of the dorsal plate (*el d p*), which descend from the epicranium. The lateral and ventral walls of the pharynx and the walls of the esophagus generally possess a well developed circularis muscle-coat and one of the most characteristic of the pharyngeal muscles is probably only a specialization of the circularis. This muscle girdles the pharynx from the angle where the crests meet, along under either crest and beneath the floor below. It may be called the girdle-muscle or cingulum (pl. 15, figs. 32, 35, *cin*). In front of the point where the cingulum passes under the floor of the pharynx, two slender muscles arise and extend back to the walls of the epicranium near the occipital foramen. These are the ventral retractors of the pharynx. They run in company with a number of slender muscles which emerge at intervals from beneath the circularis of both pharynx and esophagus. The complex that is formed by these muscles may be called the lateral dilator of the esophagus (*lat dil oes*). There are also two pairs of dilator muscles that insert on the dorsal wall of the esophagus (pl. 15, fig. 32, *ant dil, dor dil*). The larger of these lie above the supra-esophageal ganglion and closely parallel the retractors of the pharynx; the smaller lie beneath the ganglion.

When a wriggler is feeding the significance of the peculiar pharynx and musculature becomes apparent. It will be noted that the pharyngeal crests rapidly approach and separate so that the dorsal plate must be constantly infolded and withdrawn. The great fans

of flabellal setae remain spread, but sweep downward in a small arc with a flickering motion. The mandibles and maxillae are also in incessant rapid motion. At intervals the flabellae are depressed and presumably any food that may be entangled on their setae is brushed off by the maxillae. When the pharynx is filled with food, an extreme contraction occurs, the crests approach very close to one another, and the food is forced into the esophagus. The retractor muscles of the flabellae do not produce the flickering movements just described, being concerned only with depression of the flabellae. They remain tense during the gentler movements. The retractors of the pharynx and the elevators of the dorsal plate are also passive. The motion appears to be caused by a slight to and fro movement of the entire pharyngeal and buccal regions, very possibly due to activity of the epipharyngeal and lesser lateral muscles and the lateral dilators of the esophagus. The changes in the pharynx itself, as shown by the movement of the crests, can be readily interpreted. I believe that the retractors of the pharynx and the elevators of the dorsal plate remain tense. This would make the elevation of the dorsal plate largely the passive result of the divergence of the crests as the pharynx walls separate. Probably the cingulum is the most important agent in approximating the walls of the pharynx. The diagonal muscles may assist and from their crossed position should be able to exert considerable leverage. Perhaps they are the chief factor in producing the extreme compression observed when the animal swallows, for any very marked contraction of the cingulum apparently would tend to close the pharyngeo-esophageal opening.

The head of the Anopheles larva is proportionally much smaller than that of Culex and, as Nuttall and Shipley (:01–:03) have pointed out, is rounded. "In fact the diameter from above downwards is very little less than from side to side, except anteriorly, where the dorsal surface slopes downward and forward." This rostral region is narrow and compressed at the sides, and the flabellae and palatum are carried well out beyond the apices of the mandibles and maxillae. The flabellae are relatively much smaller than in Culex. Hence they recall the flabellae of the larva of Simulium, but are not stalked as are the flabellae of this genus. The maxillary palpi of the Anopheles larva are very large and conspicuous. Between the maxillae the homologue of the mental sclerite is recognizable, and in sections labial and hypopharyngeal sclerites are found.

The elongation of the rostrum and the greater rigidity of its ventral surface require a different method of feeding from that employed by the Culex larva. Nuttall and Shipley state that the maxillae, mandibles, and maxillary palp form the sides and floor of a cavity and that the flabellae "are suddenly bent back into this space, the mandibles and maxillae moving forward to meet them and at the same time opening out; they are then as suddenly released and fly back to their original position. This movement . . . . is repeated with great rapidity, often some 180 times to the minute producing a current sweeping in convergent curves towards the above mentioned cavity. From time to time the mandibles are approximated and the stiff curved hairs of their upper edge are run through the brushes" (flabellae). That this may aid in removing food from the flabellae or "brushes" is shown by the further observation that at intervals "the brushes disappear far into the mouth and are then slowly withdrawn, passing through the fine carding bristles on the inner face and anterior edge of the maxillae." In Culex, according to my observations, the food is borne into the space formed by the mandibles and maxillae by a flickering motion of the expanded flabellas and retraction of these organs is infrequent. The carding of the flabellal setae is irregular in occurrence and cannot be observed in detail owing to the unfavorable position assumed by the feeding larva. This subordinate *rôle* for the flabellae is the main difference between the feeding habit of Culex and that of Anopheles. Sections indicate that Anopheles has a pharynx of the same general form and musculature as Culex, but of relatively inferior size.

The esophagus (pl. 16, fig. 37, *oes*) has already been partly described. Its epithelium is flattened, especially toward the posterior end of the region. The chitinous intima is strong. Beneath the well developed circularis muscle-coat lies a longitudinal series of muscles, some of which emerge to form the lateral dilators of the esophagus. In the anterior part of the thorax the esophagus dips into the cardia as the esophageal valve. This valve is a deep curtain, thicker at base than at the free border. At the free border the space between the inner or direct face and the outer or reflected face is occupied by a blood sinus. Above, the space is filled by the circular fibers of the annular muscle (*ann m*). In young larvae the cells of the epithelium of the valve, except for a more columnar

aspect at the curve at the shoulder of the cardia, upper bend, are like those of the epithelium of the hinder end of the esophagus. Immediately beyond the "upper bend," the esophageal type of epithelium is succeeded by the type characteristic of the cardia and stomach. For convenience, the point where the change occurs will be called the "break" in the epithelium. In mature larvae a band of narrow columnar cells (*ann*) much like the adjacent cells of the reflected face of the valve, but staining more deeply and with more vacuolated cytoplasm, is differentiated on the valve side of the "break." This functions in the pupal stage as a regenerative ring.

Delicate longitudinal fibers pass from the esophagus across to the shoulder of the cardia (*fi*), outside the valve, as is the case with several other Dipterous larvae, but the large blood sinus found in the larva of Simulium at this point (Miall and Hammond, : 00) is poorly represented in Culex and Anopheles. Miall and Hammond also describe the fibers in the larva of Simulium as muscular. My sections and dissections of Simulium do not lend themselves to this interpretation. The fibers are evidently not muscular in Culex and those of Simulium appear to me to be similar connective elements from the sheath which encloses both esophagus and cardia. If the similar fibers in any form prove to be muscular they must not be thought of as representing the longitudinalis muscle-coat. For in Dicranota (Miall, '93) which is exceptional in having the longitudinal muscles developed over the shoulder of the cardia, these pass beneath the blood sinus. The fibers are in the usual position external to the sinus. In Simulium, Miall has observed a distribution of the intima wholly like that observed in the fresh gut of Culex. The esophageal valve of Anopheles closely resembles the valve of Culex, but has a band of longitudinal muscles within the valve between the annular muscles and the epithelial cells of the upper part of the reflected face.

The salivary duct of the Culex larva is an extremely thin-walled tube which is not differentiated at any point. It is lined with a distinct chitinous intima. It forks as the occipital foramen is passed and either branch enters a cylindrical gland. These glands taper somewhat at their proximal or duct ends. The lumen is ample and not infrequently a distension occurs at the distal end of the gland which appears in the living larva as a spherical body of high refractive index. The epithelial cells of the living gland are almost trans-

parent. In sections the cells are clearly defined, their cytoplasm stains deeply, the moderate sized nuclei (11.5 μ) are reticulate, and nucleoli are present. There are usually not more than five or six cells in the cross section at any point. As the wriggler nears the pupa stage numerous vacuoles occur in the cytoplasm of many of the gland cells, so that it appears spongy. This is a sign of degeneration. Immediately prior to pupation, a belt of small cells forms at the neck where the gland narrows to meet the salivary duct. The cells of this belt are seemingly derived from the older cells of the neck of the gland and perhaps also from the epithelium of the outer end of the duct. They give rise to the imaginal salivary glands.

The midgut.— The midgut (pl. 16, figs. 37, 45) of the larva shows three regions: cardia, a ring of eight caeca, and the stomach. The cells of the cardia stain more deeply than those of the caeca or stomach epithelium, but are otherwise similar. As already noted, the fore gut intima terminates at the "break" where the cardiac epithelium begins near the upper bend of the esophageal valve. The cardia is lined by the peritrophic membrane. In the mosquito the cardia of the larva gives rise to the cardia of the imago through a metamorphosis similar to that by which the stomach of the larva gives rise to the stomach of the adult. The esophagus and esophageal valve on the other hand, have a wholly different metamorphosis, so that in Culex the cardia would appear to be unquestionably a part of the midgut. This seems to be the case in Nematocerous flies generally, although the evidence is as yet not complete for any one form. The larva of Anopheles, Chironomus, and Simulium like that of Culex has a cardia whose epithelium resembles that of the stomach. The embryological development of the cardia of the Chironomus larva shows it to be of mesenteric origin in this case (Miall and Hammond, :00). Its relation to the cardia of the imago has not been studied. From Vaney's (:02) account it would seem that the larva of Stratiomya belongs to this type and the cardia, "proventricule," of the larva of Ptychoptera as figured by van Gehuchten ('90) is more like stomach than esophagus in the histological structure of its epithelium. Occasionally no cardia is developed and in such instances the esophageal valve hangs directly into the stomach, *e. g.* Phalacrocera (Miall and Shelford, '97) and Dicranota (Miall, '93).

The cells of the epithelium of the eight caeca are transparent, polygonal, subequal in size, and show considerable intercellular substance. The nuclei are large and have nucleoli. Although the surface of these pouches appears nodulated as if from the contraction of muscle fibers, none were found. Sections show that the cells are on the average larger than the cells of the cardia or mid-intestine and very irregular in depth. The caeca usually contain a dark ochre-colored fluid.

The stomach is cylindrical and extends back to the fourth or fifth segment of the abdomen. It is abundantly supplied with tracheae and the cells of its walls are polygonal, with granular, yellowish cytoplasm, large oval nuclei ($17 \times 10\ \mu$), and nucleoli. The cells vary greatly in size, but are of uniform depth. Like the cells of the cardia and caeca they have a striated border. The walls of the stomach are nodulated, but this seems to be due more to the irregular size of the component cells than to the contraction of muscle fibers, although scattered muscles are visible in sections. In preparations, the basement membrane is very distinct. Protrusions of cells or parts of cells into the lumen, either in fresh or sectioned material was not observed for any part of the midgut.

The above description would not be wholly applicable to the stomach and caeca at all stages. For the processes by which the epithelium is destroyed and replaced during the pupa stage begin before larval life is ended, and involve progressively more and more cells as the wriggler nears the moment of pupation. Small regenerative nuclei appear in increasing numbers between the bases of the cells of the epithelium. The cytoplasm near the free margin of the cells becomes spongy. The striated border dissolves in places and occasionally cells protrude into the lumen of the gut.

The hind gut.— In the neighborhood of the fourth and fifth segments of the abdomen the stomach narrows and the hind gut begins. This portion of the alimentary canal is divided into ileum, colon, and rectum. The ileum (pl. 16, fig. 45, *il*), extends back to the eighth joint of the abdomen and is not separated from the stomach by a valve. Probably this is in adaptation to the continuous passage of bulky wastes through the gut. In the imago, in which the meal of blood is stored in the stomach while it is being digested, a valve exists between the ileum and stomach. The freshly extracted ileum appears as if wholly composed of circular muscle fibers, is

transparent, and has an intima which is thrown into longitudinal folds. Sections demonstrate a very thin epithelium, the nuclei of the flattened cells measuring 12 by 6.5 μ. Longitudinal muscles cannot be found. For a space immediately behind the stomach the circular muscles are also wanting (pl. 16, fig. 45, x), and into this naked annulus the five Malpighian tubules empty. These tubules in every way resemble the Malpighian tubules of the perfect insect.

The second region of the hind gut, the colon (pl. 14, figs. 26, 27, *co*) is distinct from the ileum, but is not sharply marked off from the rectum. Raschke ('87) grouped colon and rectum together as "Enddarm" and Hurst's figures include both as "rectum." In the text, however, the colon would seem to make part of his "ileum." The colon lies wholly within the eighth abdominal joint. Its walls have a deep epithelium of large polygonal cells and appear to be rather unyielding. Belts of slender circular muscles occur at regular intervals, but no longitudinal muscles can be demonstrated. The living cells of the colon are granular. Sections show faint striations radiating from the region of the nucleus. The oval nuclei of the cells measure 12 by 16 μ.

Posteriorly, the colon passes gradually into the rectum (pl. 16, fig. 44, *rec*) which is wholly within the last joint of the abdomen. The rectum has delicate walls that tear easily. Sections show a very thin epithelium, resembling in structure the epithelium of the colon, and a series of regularly placed, slender, circular muscles.

The Pupa.

The first absolutely diagnostic sign of the on-coming of the pupation moult as observed in *Culex stimulans* is the appearance of two white spots in the prothorax, as the air chambers at the base of the pupal respiratory trumpets fill with air. At this moment probably the trumpets are evaginated beneath the cuticle. The larva becomes increasingly turgid in aspect and intermittent peristalsis-like waves of contraction pass over its body. The turgescence is largely due to the evagination of the pupal thoracic appendages under the cuticle. The charging of the air-sacs usually precedes the moult by about three minutes, but in one instance eight minutes elapsed, during almost all of which time the larva lay passive.

Suddenly a crack darts across the top of the head and the pale pupal head shows in the gap. From two to fifteen seconds later the cuticle of the thorax ruptures along the mid-dorsal line and the respiratory trumpets spring up to the surface of the water. The tear in the thoracic cuticle widens and the integument of the anterior abdominal rings also splits along the back as the pupa rapidly works the head and thorax clear and wriggles forward in the compressed remains of the old skin, until only the apices of the mouthparts and legs, and the tip of the abdomen are still sheathed by it. The abdomen is straight and each ring lies forward of its counterpart in the old cuticle. Hence the intima which is being withdrawn from the main longitudinal tracheae stretches back from the eighth segment to the respiratory siphon like a white cord on either side. Finally the tracheae are cleared, and the liberated pupa slips forward with flexed abdomen, rests for a few seconds, and darts away, perfectly formed, but of a light maltese color. The moult from the moment when the head cuticle splits to the clearing of the tracheal trunks has occupied from one minute five seconds, to one minute forty-five seconds. The whole process from the appearance of the air-sacs to the final darting away of the pupa takes on an average four minutes, but may occur in as short a time as two minutes or be prolonged beyond ten minutes.

The external aspect of the Culex pupa with its flattened head, high-arched thorax and nine-jointed abdomen is familiar. Male pupae can be distinguished from female by the larger gonapophyses. The gray color of the new pupa changes in an hour or so to the typical black brown. A few hours before the fly emerges the pupa becomes quite black, owing to the formation of the imaginal scale pattern under the integument. Shortly after pupation a space is formed between the integument and the dermis of the pupa (Hurst) into which the scales and hairs project. This fills with air before the fly emerges but the imago does not become much displaced in relation to the parts of the pupa skin. No violent movements precede or accompany the liberation of the fly. The abdomen of the pupa straightens and the imago quietly works itself free by slight contractions, the emergence on the average occupying four or five minutes. As much more time may elapse before the insect takes wing. I have found in Corethra and Chironomus that the space between the cuticle and the dermis fills with air prior to

the emergence of the fly as it does in Culex. I have observed the liberation of the imago of Chironomus only. Here a large amount of air is admitted under the skin, so that the pupa has a glassy appearance, the preliminary movements are prolonged and violent, and the imago becomes markedly displaced in relation to the pupal parts. The apex of the abdomen, for example, finally lies three joints cephalad of its own sheath. In one species studied, the small apple-green fly emerges so rapidly that it takes wing within fifteen or twenty seconds from the moment when the pupal cuticle first ruptures. Comparing this with the slow emergence of Culex leads me to think that a connection exists between the rapidity of the emergence, the amount of air admitted beneath the cuticle, and the relative displacement of the imago in relation to the pupal sheaths.

The mouthparts. — The mouthparts of the pupa develop during the last larval instar. The two organs that arise from invaginate imaginal buds, the labium (pl. 15, figs. 32, 34, *li*) and the maxillary palpus (pl. 15, fig. 29, *maxp bd*), appear first. The development of the labial bud may be taken as typical as regards the histological changes. The dermis beneath the labial sclerite thickens and proliferates, until a plate of minute cells, which stain deeply with haematoxylin, is formed. While steadily growing upward, this plate is depressed and finally the bud consists of a bipartite eminence arising from the floor of a deep pocket. Both pouch and eminence secrete a delicate cuticle. The labial imaginal buds of Chironomus, Anopheles, and Corethra closely resemble the bud in Culex and a similar double structure has been described for the Pupiparous fly, Melophagus (Pratt, '93). Later in the instar than the labial and palp buds, the dermis of the top of the head thickens, stains deeply with haematoxylin and grows out as a cylindrical pouch. This bud forms the labrum (pl. 15, fig. 32, *la bd*). It projects caudad, depresses the adjacent tissues and lies in a shallow mesial furrow. Of slow growth until immediately before pupation, it then elongates rapidly, and reaches back to the origin of the epipharyngeal muscles (*epi m*) before the head cuticle splits. At the same time that this bud elongates, the cells of the hypodermis of the flabellae enlarge and show a marked affinity for "orange G." The dermis then retracts, separating from the overlying cuticle. In terms of their dermis the flabellae are converted into shallow

depressions or pits in the wall of the head. The dermis of the palatum remains in position. The mandibles and maxillae undergo almost no metamorphosis prior to pupation. Shortly before the moult, their dermis thickens and takes on some of the staining reactions of the dermis of an imaginal bud, assuming a condition intermediate between the cells of the flabellal dermis and the cells of the labral, labial, or palp buds.

The larvae of Anopheles pass through a similar series of changes as far as their mouthparts are involved, so that the wrigglers of both Culex and Anopheles have at maturity an evaginate labral bud, invaginate buds for the labium and the maxillary palpi, thickened mandibular and maxillary dermis, and the dermis of the flabellae and epipharynx retracted from the cuticle. The changes beyond pupation are not known for Anopheles. With Culex, the successive alterations during the pupation moult are shown in figures 48–50 on plate 16. As the head cuticle is sloughed, the labral bud swings over into the plane of the other mouthparts. Probably its rapid growth just prior to the moult is an important factor in rupturing the head cuticle, while the change of position during pupation must assist in pushing the head case away at an angle favorable to the extraction of the ventral mouthparts (pl. 15, fig. 36). The change of position is partly due to the growth of the labrum, partly to a contraction of the retractors of the flabellae, and partly to a shortening of the dorsal wall of the buccal cavity. The moult reduces the retractor muscles to ovoid masses (pl. 17, fig. 56, *retr fl*), and shifts the flabellal depressions back to the entrance of the pharynx. The mandibles and maxillae are withdrawn as cylindrical tubes. The bud of the maxillary palpus elongates slowly at first and the labial bud has a still more tardy evagination. This is probably to allow time for the retraction of the transverse fold formed by the hypodermis of the transverse line, mental sclerite, and the front wall of the pocket of the bud (pl. 15, figs. 34, 36, *fold*).

The mouthparts of the pupa are closely pressed together (pl. 14, fig. 24) and form the central part of an ovoid shield which covers the front and sides of the body. The antennae, legs, wings, and halteres successively build the lateral parts of this shield. The shield is in close contact with the body along its borders posteriorly and ventrally, and above in front the central part is fused to the

thorax. Below in front and generally along the sides of the body an irregular space is left between body and shield. This space is filled with air (Hurst) and into it the recurved apices of the mouthparts and the folded legs project.

When the dermis shrinks away from the cuticle a few hours after pupation, the various trophi become oval or cylindrical tubes and remodeling of the imaginal forms is possible. The mandibles, maxillae, and maxillary palpi — these last occupy the same cuticular sheath as the maxillae — undergo the least modification. In male pupae the mandibular sheath was empty by the end of the first day of pupal life. During a variable period of not less than ten hours, the labrum remains circular in section. Then its ventral face becomes infolded, and through differentiation of the furrow, the proboscis canal or so called epipharynx is formed (pl. 14, fig. 24, *pc*). The labium retains a cylindric or oval cross section until near the end of the first day of pupal life. Then the dermis of the mid-dorsal face is either elevated as a low crest or proliferates and thickens (pl. 14, fig. 24, *hyp*). In both sexes cells appear in the cavity of the labium beneath the altered wall and ultimately build the salivary gutter. These cells probably arise by invagination or migration from the modified area above. After they appear, the labium of the male pupa loses the mesial differentiation and quickly moulds itself to the imaginal form, but with the female pupa the ridge or thickening finally separates from the labium as the hypopharynx (pl. 14, fig. 25). I did not succeed in obtaining sections which showed the actual separation. After disassociation, both labium and hypopharynx quickly attain the imaginal structure.

The fore gut. — Since the mouthparts of the pupa are in close contact with one another, it cannot be said that the alimentary canal is lengthened by the addition of a proboscis canal so long as the dermis lies against the cuticle of the stylets, and although represented by the intracuticular spaces between labrum and labium after their dermis has parted from the cuticle, yet the canal is not actually formed until the ventral wall of the labrum is invaginated. If a new-formed pupa be examined, the fore gut will be found empty and clean. The buccal cavity is closed by the collapse of its walls, except at the posterior end, beneath the shallow dorsal diverticula which represent the flabellae and epipharynx (pl. 15,

fig. 36, *epi*). Structureless *débris* from the strands of protoplasm that formed the cores of the epipharyngeal and flabellal setae fills the diverticula and spreads into the buccal space. In front of the curve where the potential proboscis canal enters the buccal cavity, the salivary duct opens. The pharynx retains something of the form which characterized it in the larva and the less markedly columnar epithelium as contrasted with the epithelium of the buccal cavity. The roof has evidently shortened, since the dorsal pharyngeal muscles are crowded toward the elevators of the palate, but this and other changes in the relation of organs cannot be accurately formulated, owing to the lack of fixed points from which to measure.

After the third hour of pupal life (pl. 17, fig. 56) the lumen of the buccal cavity opens again. It is soon freed from detritus and remains clean during the rest of the metamorphosis. The flabellal pits steadily diminish in size and finally fade out. The cells of the epipharyngeal pit histolyze and before the tenth hour is passed have dissolved into a mass of broken elements. This lies within the cavity of the head, completely cut off from the buccal cavity (pl. 17, fig. 57, *epi*), and is slowly absorbed without the intervention of phagocytes. Seemingly the separation of the degenerating epithelial pouch from the buccal cavity (pl. 16, fig. 39) is accomplished by an inpushing of the adjacent epithelium rather than by a proliferation of cells at the margin of the pit. Mitotic figures are absent. It is not impossible, however, that some of the epithelium which closes beneath the degenerating cells and cuts them off from the lumen of the buccal cavity is derived mediately or immediately from the epithelium of the epipharynx as it is destroyed. If this is so, and the epipharynx of the mosquito wriggler is a true epipharynx, part of the anterior hard palate of the imago is epipharyngeal in origin. And in such a case the small conical setae near its apex might gain a morphological value as epipharyngeal structures. This will not affect the character of the labrum as a simple and not a compound organ.

While the changes described have been taking place, the pharynx has become cylindrical and the cells of its epithelium now exactly resemble the cells of the epithelium of the buccal cavity. It is not clear how this alteration is accomplished. No mitotic figures can be found and no waste is given off into the lumen of the gut. The

loss of histological and structural distinctions between the buccal cavity and pharynx leaves as landmarks for the entrance to the pharynx (pl. 17, fig. 56, *) only the cingulum muscle below and the anteriormost dorsal pharyngeal muscle above. The dorsal mark is open to the objection that this muscle lies behind the actual boundary; and the relations in this neighborhood are obscured also by the retraction of the flabellal hypodermis back to the epipharynx — which does not seem to have moved much — and by the shortening of the roof of the pharynx. These criteria enable us to judge the morphological value of any comparison between the limits of the larval and imaginal fore gut regions. Nevertheless, it will be interesting and perhaps not unprofitable to work these out (pl. 17, fig. 56–58). Roughly speaking, that part of the pupal buccopharynx which is in front of the anteriormost dorsal pharyngeal muscle and the cingulum muscle represents the larval buccal cavity. Ventrally, the boundary early becomes indistinguishable owing to the loss of the cingulum muscle, but dorsally a slight bend comes in near the point where the two regions meet (*). This bend coincides with the rear border of the soft palate of the imago. Pharyngeo-esophageal boundaries are not developed in the larva ventrally, but dorsally the insertion of the retractors of the pharynx (*retr ph*) marks the rear of the pharynx. These muscles metamorphose into the ascending pharyngeal muscles of the imago (*asc ph*). The anterior dilator muscles immediately caudad become the anterior dorsal dilator muscles of the antlia of the imago. The epipharyngeal pit lies at first above and then forward of the marked curve in the gut. This curve remains after the epipharynx and its muscles have vanished and the front wall of the clypeus forms distad of it. So, unless it shifts position markedly, for which there is no evidence, the epipharyngeal muscles of the imago insert on the roof of the buccal cavity very near the point occupied by the larval epipharynx.

The esophagus undergoes no metamorphosis beyond the destruction and regeneration of the muscle-coats, the differentiation of the antlia at its anterior end (pl. 17, fig. 57), and certain changes which involve the esophageal valve. The esophageal epithelium is handed intact to the imago, probably with an increase in the number of the component cells. The muscle-coats histolyze about the eighth hour and are replaced somewhat later by the imaginal muscles. The process could not be studied in detail because of the minute size of

the new elements. The antlia gradually forms during the first half of the second day of pupal life, but in common with other parts of the alimentary canal the characteristic imaginal intima with its division into plates is not developed until just before the fly emerges. This intima is secreted beneath the delicate undifferentiated pupal intima which lines the stomodaeum. The proctodaeum similarly has a pupal intima beneath which the imaginal intima is secreted. The lumen of the esophagus remains clean during the metamorphosis, except at the posterior end, where granular rubbish containing chromatin is found, seemingly drifted in from the cardia.

All the muscles of the head continue intact until the eighth or tenth hour and then histolysis occurs. But although small leucocyte-like cells can occasionally be noted, these are rare and there is nothing which definitely assigns a phagocytic *rôle* to them. The mandibular muscles, the depressors of the antennae, the muscles of the maxilla, the epipharyngeals, the retractors of the flabellae, the diagonals, the dorsal pharyngeal muscles, the ventral retractors of the pharynx, and the cingulum histolyze and are absorbed between the tenth and thirtieth hour of pupal life. The first imaginal muscles appear about the eighth hour with two bands of small dark myoblasts, probably the maxillo-labial muscles. By the seventeenth hour the sides and floor of the head cavity are traversed by similar belts of small myoblasts. The ultimate source of the new cells is uncertain, owing to the minute size of the elements of both the larval and the imaginal muscles. From the moment of their appearance the new nuclei are closely associated with the dermis of the head and their cells resemble the small, dark cells of this epithelium. There is, however, nothing which would militate against applying van Rees' ('88) interpretation of the muscle metamorphosis of Musca to Culex. By this the new myoblasts would be derived from the nuclei of the larval muscles.

The retractors of the pharynx, the elevators of the dorsal plate, the lateral muscles, and the anterior, posterior, and lateral dilators of the esophagus are worked over into imaginal muscles. The anterior esophageal dilators alter first and their metamorphosis may be taken as typical. A majority of the large reticulate nuclei become smaller, darken, and lose the reticulum; others histolyze. Then a large number of small dark nuclei appear, perhaps derived from the older muscle nuclei by amitotic division. The two sets of

nuclei, older and younger, remain side by side until the twentieth hour is reached, when the contractile substance, hitherto hostile to haematoxylin, stains readily with it and all the nuclei are larger and reticulate — the imaginal condition. The final increase in the amount of the contractile substance and the complete attainment of the imaginal staining reaction are soon reached. The relation of the larval to the imaginal muscles is as follows: —

Larval Series.	Imaginal Series.
Retractors of the pharynx.	Ascending pharyngeals.
Lateral muscles of pharynx.	Lateral pharyngeals.
Elevators of the dorsal plate.	Muscles of the valve.
Anterior dilators of the esophagus.	Anterior dorsal dilators of antlia.
Posterior dilators of the esophagus.	Posterior dorsal dilators of antlia.
Lateral dilators of the esophagus.	Lateral dilators of antlia.

Probably only the posterior portion of the muscle complex that I have called the lateral dilator of the esophagus, gives rise to the lateral dilator muscles of the imago's antlia, the anterior portion being histolyzed. The hypopharyngeal muscles of the adult are derived from the fibers beneath the hypopharyngeal sclerite. Those muscles dorsad of the alimentary canal which have forerunners among the larval muscles appear from the twenty-fifth hour onward and the clypeus begins to differentiate at this time (pl. 17, fig. 58).

The esophageal valve of the new-formed pupa is partly drawn out of the cardia, so that the annulus of regenerative cells (*ann*) lies in line with the walls of the cardia and the upper bend of the valve has been shifted to a point low down on the reflected face. The regenerative annulus also has widened, probably through modification of adjacent cells of the epithelium of the valve. In a pupa five hours old (pl. 16, fig. 38) the valve is completely withdrawn from the cardia. The regenerative annulus is very prominent and the annular muscle of the valve (*ann m*) has begun to degenerate in advance of the histolysis of the muscle-coats generally. An hour later, the regenerative annulus is represented by a low circular ridge of columnar cells which projects into the lumen of the esophagus just above the cardia. The valve lies immediately cephalad as a low ring-fold of the wall of the gut, girdled externally by the

remains of the annular muscles. By the tenth hour (pl. 16, fig. 43) the parts are hardly recognizable; for the valve (*v*) is flattened and almost obliterated while the cells of the annulus (*ann*) have largely lost their characteristic histological structure and resemble cells of the adjacent esophageal epithelium. The eleventh-hour pupa has almost the imaginal relations (pl. 16, fig. 40). The regenerative ring and larval valve have disappeared, the epithelium is everywhere of esophageal type and near the cardia the walls are folding inward to build the imaginal esophageal valve. The rapidly diminishing belt of *débris* which remains from the degenerated annular muscles lies cephalad of the new valve. The infolded region clearly is epithelium that at one time formed part of the regenerative annulus.

At about the tenth or eleventh hour the esophageal diverticula push out just caudad of the histolyzed annular muscles. They probably do not involve cells that have formed part of the regenerative annulus, but arise from esophageal epithelium which has not been altered (pl. 16, figs. 40, 43, *f res*). The out-pushings quickly enlarge to small pouches, the ventral one opening widely into the lumen of the gut, the dorso-lateral ones with narrow stalks. Growth is then slow until the thirtieth hour of pupal existence, after which the pouches rapidly attain the respective imaginal proportions. The epithelium remains like that of the esophagus, columnar, till the very end of pupal life, when the characteristic imaginal epithelium is developed, seemingly by a flattening of the cells, accompanied by a folding and wrinkling of the walls. I am not certain whether these pouches secrete a pupal as well as an imaginal intima. When the mosquito leaves the pupa case the sacs are empty, but air bubbles appear shortly after emergence.

It is not possible to escape the feeling that a relation exists between the formation in Culex of the annulus of regenerative cells close to the cardia and the development of the "anterior imaginal ring" at the same point during the metamorphosis of other flies. Such a ring of regenerative cells has been described for Chironomus, Anthyomyia, Stratiomya, Tanypus, Gastrophilus, and Musca (Vaney, :02). Its fate has been determined for Gastrophilus and Musca. In the former the whole stomodaeum is destroyed and is replaced "entirely by proliferation of cells derived from the buccal discs and the interior imaginal ring" (Vaney, :02). With Musca

the stomodaeal epithelium is partially destroyed at least and is rebuilt from scattered regenerative cells, as well as from the imaginal ring (van Rees, '88). In Culex the esophageal epithelium seems to suffer no loss of cells and the regenerative annulus gives rise to the imaginal esophageal valve by simple remodeling.

The salivary glands frequently begin to degenerate before pupation occurs and the destructive processes advance rapidly during the first hours of pupal life. The cytoplasm of the epithelial cells becomes more and more spongy, large vacuoles appear here and there, and the nuclei decrease in size. Meanwhile the small regenerative cells at the neck of the gland are steadily increasing in number. By the twentieth hour the glands have shifted to a more ventral position and the regenerative epithelium stains deeply with haematoxylin, a characteristic of regenerative epithelium generally. The nuclei of the gland cells are now still more diminished in size and the vacuolization is extensive, especially near the belt of regenerative cells. Frequently cells are so distended by vacuoles that they obliterate the lumen of the gland. About this time the imaginal salivary glands appear as three small cylinders developed from the regenerative epithelium. As soon as these form, the larval glands histolyze completely, become a mass of granular detritus filled with fragments of chromatin and are absorbed without phagocytosis in five or six hours. In their places on either side of the thorax lie the three slender tubes of the imaginal glands. Just before the mosquito leaves the pupa case the glands enlarge, shift to the adult position beneath the alimentary canal, and the central and lateral acini become unlike. Whether the final increase in size is due to increase in the number of component cells or only to growth of cells already present, could not be determined. After the emergence of the fly, the nuclei of the cells enlarge slightly, and the cells become distended with the stored salivary secretions until three times their former dimensions.

The epithelium of the cardia and stomach is totally histolyzed and a new epithelium is formed from regenerative nuclei which appear among the older cells. This course of development has been observed for the midgut of all flies whose metamorphosis has been studied (Korscheldt and Heider, '99). The larva of Culex reaches pupation with degenerative and regenerative processes well established. The cytoplasm of the epithelial cells is vacuolated,

producing a spongy appearance, the striated border is dissolving, and occasionally cells protrude into the lumen of the canal. Between the bases of the older cells the regenerative nuclei occur in increasing numbers. With the larvae of *Tenebrio molitor* (van Rees, '88) the regenerative nuclei are found even in the first instar. I do not know how early they appear with the mosquito wriggler. In the last larval instar and the newly formed pupa they are very numerous. As these nuclei increase in number, they diminish in size, which suggests that they are derived by repeated divisions from those present in the larval stage.

The changes advance swiftly after pupation. In a pupa one hour old (pl. 14, fig. 28) the epithelial cells are separating from one another, are elongate and protrude into the lumen, the striated border has been everywhere lost, and the cytoplasm is dissolving. By the third hour of pupal life, the regenerative nuclei, which are now about the size of the epithelial cells of the gut of the imago — less than one half as large as the regenerative nuclei of the larva — have forced the older cells from the basement membrane and form a definite pavement epithelium with recognizable cytoplasm. The older cells lie in fused masses in the lumen of the gut, their nuclei reduced to dark granulate spheres. Here they are rapidly absorbed (pl. 16, figs. 40, 43, *ca*). This metamorphosis does not proceed with equal celerity in all regions of the midgut. The caeca, the cardia, and the iliac end of the stomach lag behind the major part of the stomach. The caeca decrease in size as their epithelium histolyzes, and by the fifteenth hour they have vanished. The epithelium of the cardia degenerates first at the posterior end of the chamber. The new epithelium, unlike that of the caeca and the stomach, consists of columnar cells from the beginning and appears to be formed as an advance forward beneath the older cells (pl. 16, fig. 38, *ca*), instead of simultaneously over all parts of the wall.

At the beginning of pupal life the hind gut regions, ileum, colon, and rectum are the same as in the mature larva, except that they are shortened and that a ring of small dark cells lies between the rectum and the anus (pl. 17, fig. 54, *r an*). This ring develops during pupation and the first hour of pupal life, but whether its cells are derived from the cells of the posterior end of the rectum or from cells of the hypodermis in the region of the anus could not be determined. The rectum and ileum are involved in degenerative

and regenerative processes which run the same course in all parts of both regions, but could only be studied in detail for the ileum. The metamorphosis of the colon is very peculiar.

According to Hurst ('96) the epithelium of the intestine "divides into a thin outer and a thick inner layer. The latter becomes loosened, breaks up and appears to be digested." The process for the species of Culex that I studied is not as simple as this would imply. The flattened epithelium first becomes columnar. Then the cells degenerate, separating more or less from one another. Large vacuoles make their appearance, the cytoplasm becomes spongy, and a small amount of *débris*, in which granules of chromatic material are noticeable, is given off into the lumen of the canal. In all regions considerable mitosis was observed toward the end of the changes. The processes begin at the upper end of the ileum, run their course here in about six hours and then involve simultaneously the rest of the ileum and the rectum, lasting eight or ten hours. They result in the formation of an epithelium of small, dark-staining cells, somewhat like the cells of the new anal ring. These gradually alter to the adult characters for each region. Enlargement and probably proliferation of cells in certain parts of the rectal walls form the rectal papillae (pl. 17, fig. 53, *p*). The muscle-coats are lost about the seventeenth hour and are later replaced by new muscles.

It is evident that in the metamorphosis of the ileum and rectum certain of the epithelial cells are eliminated and new cells, derived from epithelium which escapes destruction, replace them. Probably the degenerative process involves all the older cells to a greater or less degree. The nuclei of the reconstructed epithelium are barely one half the size of the nuclei of the older cells. The nature of the preliminary alteration by which the epithelium becomes columnar is obscure. It does not seem, however, to depend on any contraction of the walls of the gut.

The alterations recorded above are not without relation to the postembryonic development of the hind gut in such flies as Musca or Gastrophilus. In the latter genus, the hind gut is destroyed and is reconstructed from an anterior imaginal ring of regenerative cells near the Malpighian tubules and a posterior ring near the anus (Vaney, : 02). The hind gut of Musca evidently undergoes a similar metamorphosis, but observers do not agree as to the amount of epithelium destroyed. Kowalevsky ('87) asserts that all the older

cells are swept away while van Rees ('88) believes that a considerable part of the older wall remains. In Culex the appearance of the regenerative changes in the neighborhood of the Malpighian tubules before the remainder of the gut is involved, and the formation of an anal ring of new cells — whatever their ultimate source — furnish interesting parallels to the conditions found in Musca and Gastrophilus. The resemblances of course mean no more than the presentation in varied degree of certain tendencies which exist among the Diptera. A closer genetic connection is not implied.

As an illustration of the improbability of such a connection we may take the changes which occur in the colon of Culex. The development of this region recalls the reconstruction of the hind gut in the more specialized flies from anlagen at either end of the canal. But the processes are not really comparable with those found in Musca or Gastrophilus and when we consider the simple metamorphosis of the remaining hind gut there is marked and peculiar specialization. The colon of Culex is destroyed and replaced by a tube formed from a backward growth of the cells of the ileum and a forward growth of the cells of the rectum. The proliferation begins as soon as the iliac and rectal epithelia are reconstructed, *i. e.*, about the seventeenth hour. At this time the cells of the shrunken colon are spongy, and have separated from one another. Their nuclei have diminished in size but are intact (pl. 17, fig. 52, *co*). The invading cells enter the lumen (pl. 17, fig. 59), and active mitosis is observable at and near the head of either advance. The two cell armies seem to progress with equal speed. As soon as the advance is well under way, the nuclei of the colon cells lose their reticular structure and reduce to masses of chromatic material within the nuclear membranes. Nuclei and cells, however, remain distinct until individually displaced by the invading cells, and then quickly histolyze. In a nineteen-hour pupa, cells already displaced lay outside of the new epithelium as a mass of fragments, while cells still in position remained distinct units. By the twentieth hour of pupal life (pl. 17, fig. 53) the new canal (*ilc*) is completed and the old colon (*co*) is represented by *débris*. This is quickly absorbed without the intervention of phagocytes. The muscles of the larval colon histolyze *in situ*. The muscles of the new ileo-colon are developed from myoblasts, probably from the ileum and rectum.

The Malpighian tubules pass from the larva to the imago without visible change. This absence of metamorphosis appears to be the rule for these tubules in the Nematocerous Diptera, if observations on Simulium, Chironomus, and Psychoda (Vaney, :02) added to those for Culex, give a sufficient basis for generalization.

Notes on the metamorphosis. — The organs of Culex outside of the alimentary canal undergo a metamorphosis as simple in grade as that of the mouthparts or alimentary canal. A few points with respect to these organs may be noted. The dermis of the head and the body is passed directly over to the imago. The muscles of the thorax and abdomen also are seemingly not involved in any alterations. The wing and leg muscles are new with the pupa, the rudiments of the former being present beneath the hypodermis of the dorsum of the thorax during the last larval instar. My observations on the fat body accord with those of Vaney. "In the lower Diptera (Culex, Simulia, Chironomus) the fat elements are maintained in their integrity from the larva to the adult." In the fat body dorsad of the nerve cord in the abdomen, there can be noted during the pupal stage scattered cells which resemble leucocytes more than other cells of the body. These do not, however, appear to function in any manner.

The eyes of the larva form part of the compound eyes of the perfect insect. Hurst ('90) has given a good account of the evolution of the imaginal eye, which "consists in the addition of new elements at the edge [of the larval eye] which arise by direct modification of the . . . . epidermis around the margin of the eye, epidermis whose last function was to secrete the pupal cuticle." He notes that "corneal facets are never formed in the pupal cuticle" and that the ocellus of the larva is inconspicuous in the adult. I find that this ocellus degenerates during the pupa stage. The cells become vacuolated, the pigment agglomerates, and the whole structure sinks beneath the dermis. In the perfect insect each ocellus is hardly more than a small mass of black pigment at the rear of the compound eye.

Both Culex and Anopheles have a pair of rudimentary ocelli which do not seem to have been described. They are situated on the vertex of the head, caudad and mesad of the bases of the antennae. Each consists of a plate of enlarged dermal cells, lying immediately over a small ganglionic mass of spindle-shaped cells. A fine nerve

connects this ganglion with the supra-esophageal ganglion. The overlying cuticle is not modified (pl. 12, fig. 2 ; pl. 13, fig. 8, *oc*). These ocelli are not present in the larva, but develop during the pupation moult. Probably they represent in a vestigial form the lateral members of the three ocelli found on the head of many Nematocerous flies. If this is the case, no trace of the median member can be found.

During the pupal stage the nervous system undergoes gradual changes which are growth rather than a metamorphosis, increasing greatly in size and probably also in complexity. The brain of the imago is relatively enormous and there are two huge optic ganglia united above to the supra-esophageal ganglion (pl. 13, fig. 9–11, *o gang*). A small buccal ganglion lies above the pharynx, between the last pair of elevators of the palate and the valvular muscles. The larva, on the other hand, has a small, transverse supra-esophageal ganglion and an insignificant infra-esophageal ganglion (pl. 15, figs. 29, 30). The swollen lateral apices of the supra-esophageal mass correspond to the optic ganglia of the imago (*o gang*). The buccal ganglion is very small (pl. 15, fig. 32, *b gang*). The thoracic ganglia of the imago are united to form a single elongate mass. In the abdomen six ganglia are distinct and occupy the joints from the second to the seventh inclusive. In the larvae, however, (pl. 14, fig. 26) there are three separate thoracic ganglia and the first eight abdominal joints are furnished with a ganglion apiece. During the later larval instars, the ganglia of the first and eighth joints of the abdomen shift to the anterior borders of their respective segments, and before pupation occurs, the ganglion of the first joint enters the thorax (pl. 17, fig. 54). Later, it fuses with the thoracic ganglia to form the thoracic ganglion mass. Some hours after pupation, the ganglion of the eighth abdominal segment passes into the seventh joint (pl. 17, fig. 55) and ultimately fuses with the ganglion already present in the segment to form the sixth abdominal ganglion of the imago.

The imaginal buds share in the simplicity of the metamorphosis. With the exception of those for the antennae, none are deeply invaginated, and as far as the mandibles, maxillae, and the tail fans of the pupa are concerned, the formative dermis does not alter beyond the thickening which is the invariable preliminary to the formation of an imaginal bud. The labium, maxillary palpi, tho-

racic limbs, respiratory trumpets, wings, halteres, and gonapophyses are developed from shallow invaginate buds. The labrum is formed from an evaginate bud. The thoracic and antennal buds are evaginated immediately prior to the pupation moult (pl. 16, fig. 48), the labial and maxillary palp buds after the larval cuticle is partly removed. The buds for the gonapophyses are situated on the ventral face of the ninth joint of the abdomen. The patches of altered hypodermis which represent in a rudimentary form buds for the tail fans of the pupa are formed low down on the sides of the eighth segment of the abdomen. In the species of mosquito studied by Hurst these buds are described as "plate-like bodies lying immediately beneath the cuticle of the larval siphon." They lie high up on the sides of the segment in the larva of Anopheles, and in Corethra are almost dorsal in position. These differences are probably correlated with the varied size and shape of the eighth abdominal segment in the three genera: wide and unincumbered in Corethra, narrower in Anopheles with a small dorsal respiratory siphon, and very narrow in Culex with a huge dorsal siphon. The tail fan buds are the last to appear in the Culex larva. The order for the development of the imaginal buds is: antennal and thoracic; labial and maxillary palp; labral; gonapophysial; mandibular and maxillary; tail fan.

The antennal buds are of especial interest. They are deeply invaginated into the head cavity, and when completed the base of the new antenna at the bottom of the invagination pocket lies behind the eye spot (pl. 15, fig. 29, *ant bd*). Miall and Hammond ('92) compare the type of antennal and eye development presented by Culex, where the eyes are maintained independently of the antennal invaginations, with that found in Chironomus or Simulium where invaginations give rise to both antenna and eye, and finally with the extensive invaginations of Musca from which eye, antenna, and the whole head are formed: the so called "brain appendages." On a basis of this comparison he places Culex at the bottom of a series, Simulium and Chironomus higher, and Musca at the summit. This arrangement is perhaps justified as a statement of progressive elaboration of a tendency to form eye and head from an invagination that is connected with the antennal bud. But it does not sufficiently accentuate the mechanical aspects of the phenomenon. Kellogg (:02) appears to me to express the case better when he

says: "Whether an organ, as wing, leg, antenna, or mouthpart, shall begin as an invagination or an evagination of the derm is chiefly a matter of mechanical necessity or ease and of the radicalness of the metamorphosis." The "brain appendages" of Musca, the deep cephalic pouches of Chironomus, the shallow cephalic pouches of Simulium, and the independent eye and antennal formation of Culex do not constitute a closely locked series. The character and position of the invagination differ in each instance. The genera can be compared only with respect to the radicalness of the metamorphosis in each case, by which varied modifications of tendencies that exist throughout the Diptera are presented. That mechanical necessities are more potent than relationship in determining the character of a bud is well shown by a comparison of the antennal buds of Culex, Anopheles, and Corethra. The larva of the first genus has a broad, capacious head, but the head of the larva of Anopheles is laterally compressed, and that of the Corethra larva is markedly flattened from side to side. The antennal buds in Culex are thrust back into the cavity of the head. In the other genera the antennal buds are thrust back in deep longitudinal furrows on either side of the head, and the invagination pocket is narrowly open for its entire length.

Summary.

The alimentary canal of the mosquito has a midgut and hind gut which are not subdivided into numerous or well defined regions, but the fore gut exhibits the maximum amount of differentiation that has been found among the flies. It may be divided into proboscis canal, pharynx, antlia, and esophagus. The pharynx and antlia are pumping organs. Their suctorial action depends on the modification of the chitinous intima to form definite areas or "plates," which spring inward and occlude the lumen, to be withdrawn again by muscles. This duplication of the pumping apparatus places the mosquitoes in the diantlial class of flies, a group which probably includes all the Nematocera. The Muscidae and others of the Cyclorrhapha are monantlial, having only the anterior or pharyngeal pump. There is no secondary union of the pharynx with the walls of the head, so that it is not converted into a fulcrum. In this region, as is the case

with all other flies, the walls and floor are rigid and the dorsal roof constitutes the plunger of the pump. The pyriform antlia on the other hand has walls that are modified to form three racquet-shaped plates, one dorsal, two ventro-lateral. In the narrower anterior end of the pump, forward of the circumesophageal nerve-ring, the walls become unyielding, so that the dorsal plate alone retains a limited amount of motion. In correlation with the inactivity of this part of the pump the anterior dorsal dilator muscles are vestigial. The Anopheles mosquitoes, which otherwise closely resemble the members of the genus Culex in the structure of their fore gut, have a more cylindrical antlia, the anterior end of which is much less rigid, and the dilator muscles are well developed. A valve separates the pharynx from the antlia and a sphincter muscle surrounds the rear of the latter pump as it gives place to the esophagus. The esophagus is a thin-walled tube with flattened epithelium and poorly developed muscle-coats. The esophageal valve is small and immediately in front of it the three esophageal diverticula arise. The tracheal supply to the fore gut is scanty, but the number of branches which run to the muscles of the pharynx and antlia indicate great activity for both pumps.

Each of the two salivary glands is composed of three acini, the middle member being unlike the lateral in the character of its secretions. The ducts from these glands unite in the rear of the head and the resulting median duct empties into a cup-shaped chitinous pump at the base of the hypopharynx. This pump forces the saliva along the salivary gutter of the hypopharynx into the wound.

The two regions into which the midgut may be divided, the cardia and the stomach, are not sharply distinguished from each other. Their epithelium is low and columnar, the muscle-coats are represented by slender longitudinal and circular muscles, and caecal pouches are not developed. This last is a point of difference between Culex and Anopheles, as the latter genus seems to possess rudiments of such diverticula. The tracheal supply to both cardia and stomach is extensive and the abdominal portion of the stomach is capable of great dilatation, serving as a storage place for the meal of blood while it is being digested.

A prominent valve is developed at the posterior end of the stomach, opposed to a similar valve at the upper end of the first

region of the hind gut, the ileo-colon. Between the two sets of valves the orifices of the five Malpighian tubules are situated. The two regions of the hind gut, the ileo-colon and the rectum, are distinguished mainly by the greater diameter of the latter and the six rectal papillae on its walls. The epithelium is uniformly flattened, the muscles are much like those of the stomach or cardia, and the tracheal supply is extensive. A thin chitinous intima lines the hind gut, and is differentiated to form a hirsute belt immediately behind the valve at the upper end of the ileo-colon.

The regions to the alimentary canal of the imago and larva are noticeably unlike in several points, and the high degree of adaptability of the Dipterous larva generally, has produced within the group marked variations in the morphology of the alimentary tracts in the young of closely allied genera. Hence in a sense, the morphology of the larval and imaginal gut are separate problems. In the larva of Culex or Anopheles the following regions can be distinguished: buccal cavity, pharynx, esophagus, cardia, stomach, ileum, colon, and rectum. Of these, the pharynx is not well marked off from the esophagus below and at the sides, the cardia is more distinct from the stomach than in the imago, but clearly a differentiation of its anterior end, and the colon and rectum pass gradually into one another.

The buccal cavity has columnar epithelium and an epipharynx is differentiated on its dorsal wall. The epithelium of the pharynx is flattened. This region has the heaviest intima of any part of the larval gut and is an organ of peculiar shape with an elaborate musculature. The buccal cavity of the larva corresponds to the posterior end of the proboscis canal and the anterior two thirds of the pharynx of the imago. The pharynx of the larva forms the posterior third of the pharynx of the fly, while the anterior end of the esophagus becomes the antlia. The esophagus has flattened epithelium, strong circular, and well developed longitudinal muscles. Esophageal diverticula are lacking, but the esophageal valve is more highly specialized than the corresponding valve of the imago. It is less modified, however, than the esophageal valve of the larva of Anopheles, the alimentary canal of which otherwise closely resembles that of Culex. The salivary glands of the mosquito wriggler are cylindrical and the salivary duct is undifferentiated throughout its length. It opens freely on a small area of heavy chitin in the

floor of the buccal cavity, the hypopharyngeal sclerite. This structure is not homologous with the hypopharynx of the imago.

The epithelium of the cardia and stomach is very unlike that of the same regions with the perfect insect, being composed of large polygonal cells which have a striated border and large nuclei. Eight cylindrical caeca protrude in a circle just behind the cardia and there is no valve at the posterior end of the stomach nor at the cephalic end of the ileum. The muscle-coats are weak.

Of the three regions of the hind gut, the ileum has an extremely thin epithelium and well developed circularis muscles, the colon an epithelium of huge polygonal cells and slender belts of circular muscles at intervals, while the rectum has a very thin epithelium indistinguishable from that of the colon and similar belts of circular muscles. The hind gut is lined by a strong chitinous intima.

The metamorphosis of the mosquitoes as shown by Culex is of low grade compared to that of other flies. No phagocytosis has been observed. The fat body, the Malpighian tubules, the ventral thoracic muscles, and the muscles of the abdomen seemingly are passed on intact to the imago. The eyes of the larva are the eyes of the pupa and are elaborated to form part of the compound eyes of the adult, the remainder of these organs being developed from the surrounding hypodermis. The larval ocelli degenerate. The nervous system increases greatly in bulk and complexity, two of the abdominal series of ganglia change their position, a Johnston's organ is formed within either antenna, and two vestigial ocelli appear on the vertex of the head. These changes are rather of the nature of growth than metamorphosis. The dermis of the head and body moulds itself to the pupal and imaginal contours and secretes the successive pupal and imaginal cuticular structures without visible mitosis or histolysis. The epithelium of the fore gut alters greatly in appearance, the pharyngeal and antlial pumps are differentiated, the larval esophageal valve fades away and a new valve is formed by the out-folding of the gut walls, and the esophageal diverticula are pushed out. Apparently the epipharynx alone undergoes histolysis during these changes.

No true imaginal buds are developed for the mandibles, the maxillae, or the tail fans of the pupa. The hypodermis merely thickens and stains more deeply. The labrum develops as an evaginate pouch of altered hypodermis on top of the head. The labium,

maxillary palpi, thoracic limbs, wings, halteres, and gonapophyses are developed as invaginate buds. But the invaginations are very shallow in most cases and in the deepest of them — those for the antennae — the connection with the surface of the head is a wide channel. During the pupal stage the hypodermis of the mid-dorsal face of the labium thickens and forms a low ridge, beneath which cells build the salivary gutter. In male pupae the ridge disappears as soon as the salivary gutter is formed. In female pupae it separates from the labium and becomes the hypopharynx.

The longitudinal and circular muscles of the walls of the alimentary canal and most of the head muscles are completely histolyzed. It seems likely, however, that the head muscles and the muscles of the walls of the gut in the perfect insect are derived from myoblasts which are descendants of nuclei of the older muscles. A few of the muscles in the head undergo a partial degeneration only and in a sense give rise directly to imaginal bands. The muscles of the wings and legs of the imago are new with the pupa stage. The rudiments of the former series appear during the last part of the larval period.

The epithelium of the midgut, *i. e.*, of cardia, caeca, and stomach, is sloughed and is replaced by a new epithelium derived from scattered regenerative cells. These appear during the larval stage, multiply rapidly, and during the early part of the pupal stage form an epithelium which displaces the older cells. The latter fall into the lumen and are absorbed. The larval colon is completely histolyzed and a canal which grows into its lumen by proliferation of cells of both ileum and rectum replaces it. Prior to this growth, the epithelium of the ileum undergoes a partial degeneration. Hence the posterior end of the imaginal ileo-colon is a new structure. The anterior end consists mainly of remodeled cells of the older epithelium. In the rectum the anterior portion has a metamorphosis similar to that of the ileum. The posterior end is rebuilt from an anal ring of regenerative cells the origin of which is uncertain.

The metamorphosis of the alimentary canal of Culex presents parallels to the postembryonic development of the most specialized flies. Thus, a belt of differentiated cells forms near the cardiac end of the fore gut, recalling in its position the anterior imaginal ring of Musca, from which much of the foregut of the imago is derived. In Culex the ring is remodeled to form the esophageal valve. The anal ring

already noted, from which part of the rectum comes, and the fact that the degenerative and regenerative processes in the epithelium of the ileum commence and are completed near the Malpighian tubules before they involve the rest of the hind gut, recall the positions of the anterior and posterior imaginal rings in the postgut of many flies. Even the peculiar metamorphosis of the colon may be compared with the formation of the hind gut in the specialized Cyclorrhapha by a forward growth from the anal and a backward growth from the Malpighian regenerative rings, whether the older epithelium is destroyed completely as in Gastrophilus, or partly as in Musca. The alterations of the midgut also are precisely the same as those which are found in all flies, even the most specialized.

Moreover, comparisons may be made for other organs than those of the alimentary canal. For example, on the basis of the antennal buds, a series of genera may be formed, beginning with Culex, where the larval — and pupal — eye is independent of the antennal bud, through flies where the eyes develop from the same invaginations as the antennal buds, up to Musca, a species in which the whole head is formed from a pair of large invaginations. But all such comparisons must be taken to mean no more than this, that Culex and the other flies present in varying degree and under varying conditions, tendencies common to the insect group of which they are representatives.

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EXPLANATION OF PLATES.

All figures, unless otherwise specified, are drawn from camera outlines and represent Culex.

Abbreviations.

ann, ring of regenerative cells below esophageal valve.
ann m, annular muscle of esophageal valve.
ant, antenna.
ant bd, antennal bud.
ant dil, anterior dorsal dilator muscle of antlia.
ant hd p, anterior hard palate.
ant m, antennal muscle.
apo, apodeme of maxilla (imago).
apo, apodeme supporting pharynx wall (larva).
asc ph, ascending pharyngeal muscle.
bc, buccal cavity.
b gang, buccal ganglion.
blks, black spot area of larval head.
bord l, bordering line of larval head.
ca, cardia.
cae, caeca of stomach.
cin, cingulum muscle.
co, colon.
conv mnd, converger muscle of mandible.
cres, crescentic sclerite of pharynx roof.
cu, "cushion" at entrance to pharynx.
dep li, depressor of labium.
dep max, depressor of the maxilla.
diag, diagonal muscle.
div mnd, divaricator of the mandible.
do retr, double retractor muscle.
dor dil, posterior dorsal dilator muscle of antlia.
dor ph, dorsal muscles of pharynx.
el d p, elevator muscles of dorsal plate.
el pal m, elevator muscles of the palate.
epi, epipharynx.
epi m, epipharyngeal muscles.
epi tr, epipharyngeal traverse.
ext tra, external trachea.
fi, fibers passing from esophagus to shoulder of cardia.
fl, flabella.
fold, "fold" in front of labial bud.
f res, esophageal diverticula.
gang, brain.
h tr, traverse to hypopharynx and pharynx.
hyp, hypopharynx (imago).
hyp, hypopharyngeal sclerite (larva).
hyp m, hypopharyngeal muscles.
il, ileum.
ilc, ileo-colon.
in ant, inner muscle of antenna.
int tra, internal trachea.
ir fl, insertion inner retractor flabellae.
la, labrum.
la bd, labral bud.
la m, labral muscle.
lat dil, lateral dilator muscles of antlia.
lat dil oes. lateral dilator of esophagus.
lat m, lateral muscles of pharynx of larva.
lat ph, lateral pharyngeal muscles.
less lat, lesser lateral muscles.
li, labium.
li n, labial nerve.
li tra, labial trachea.
m, circularis muscle of colon (larva).
mal t, Malpighian tubules.

max, maxilla.
max-li, maxillo-labial muscle.
maxp, maxillary palpus.
maxp bd, bud of maxillary palpus.
mnd, mandible.
mnd m, mandibular muscle.
o gang, optic ganglion.
oc, ocellus.
oes, esophagus.
or fl, insertion outer retractor flabellae.
ou ant, outer muscle of antenna.
pal, palatum.
pc, proboscis canal.
per, peritrophic membrane.
ph, pharynx.
prot max, protractor of the maxilla.
pump, antlia.
r ann, ring of new cells near anus.
rec, rectum.
retr fl, retractor muscles of flabellae.
retr max, retractor muscle of the maxilla.
retr ph, retractors of pharynx.
s pump, salivary pump.
sca, scythe-shaped thickening on head.
sd, salivary duct.
sg, salivary glands.
s-o m, subocular muscle.
sph m, sphincter muscle of antlia.
st, stomach or midintestine.
tent, tentorium.
tent m, tentorial muscle.
tr, mental sclerite ("black triangle").
tr l, "transverse line".
ub, "upper bend" of esophageal valve.
v, esophageal valve.
val m, valvular muscle.
vent r ph, ventral retractors of pharynx.

PLATE 12.

Fig. 1. Pharynx and salivary pump of female mosquito; seen partly in section and partly in surface view.

Fig. 2. Semi-diagrammatic section of head of female mosquito, showing pharynx, antlia, and muscles. The section is supposed to pass near the midline above and anteriorly. It cuts across the base of the maxillary palp (*mxp*). the "head" of the tentorium of the left side, and then sweeps outward to the origin of the lateral dilator muscles (*lat dil*). The labium is sectioned along the midline. Only the proximal ends of the mouthparts are shown. On the "head" of the tentorium the origin of the inner (*in ant*) and outer muscles of the antenna can be noted. A portion of the retractor of the maxilla (*retr max*) is removed near the origin of the muscle to display the insertions of the protractor of the maxilla (*prot max*) and the maxillo-labial muscles (*max-li*) on the free end of the maxillary apodeme (*apo*). The anterior end of the retractor muscles and apodeme are removed to show the insertion of the double retractor muscle (*do retr*) on the articular spur of the maxilla and the attachment of the hypopharyngeal muscle (*hyp m*) to the salivary pump. The origin end of the hypopharyngeal muscle can be seen on the pharynx wall above the double retractor. The brain is sectioned, and the buccal ganglion (*b gang*), labial nerve, and one of the rudimentary ocelli (*oc*) are indicated. The left member of each pair of the elevators of the palate on the roof of the pharynx and of the pair of valvular muscles dorsad to the buccal ganglion at the entrance to the antlia has been cut off, leaving the muscles of the right side in place. The labral muscles in the clypeus also have been partly removed (*la m*). Behind the ascending pharyngeal muscles which bind the posterior ends of the pharynx to the vertex of the head (*asc ph*) part of the vestigial anterior dorsal dilator muscle of the antlia is visible. Below, the lateral pharyngeal muscle can be seen, passing from the outer face of the articular spur of the pharynx to the upper end of the tentorium. All the mandibular muscle, which runs from the "head" of the tentorium to the mandible, is removed except the insertion end (*mnd m*) and below this can be seen the small maxillary muscle which extends from the wall of the pharynx to the maxilla. The slender tentorial muscle parallels the nerve cord and runs back into the thorax. The minute subocular muscle is not figured.

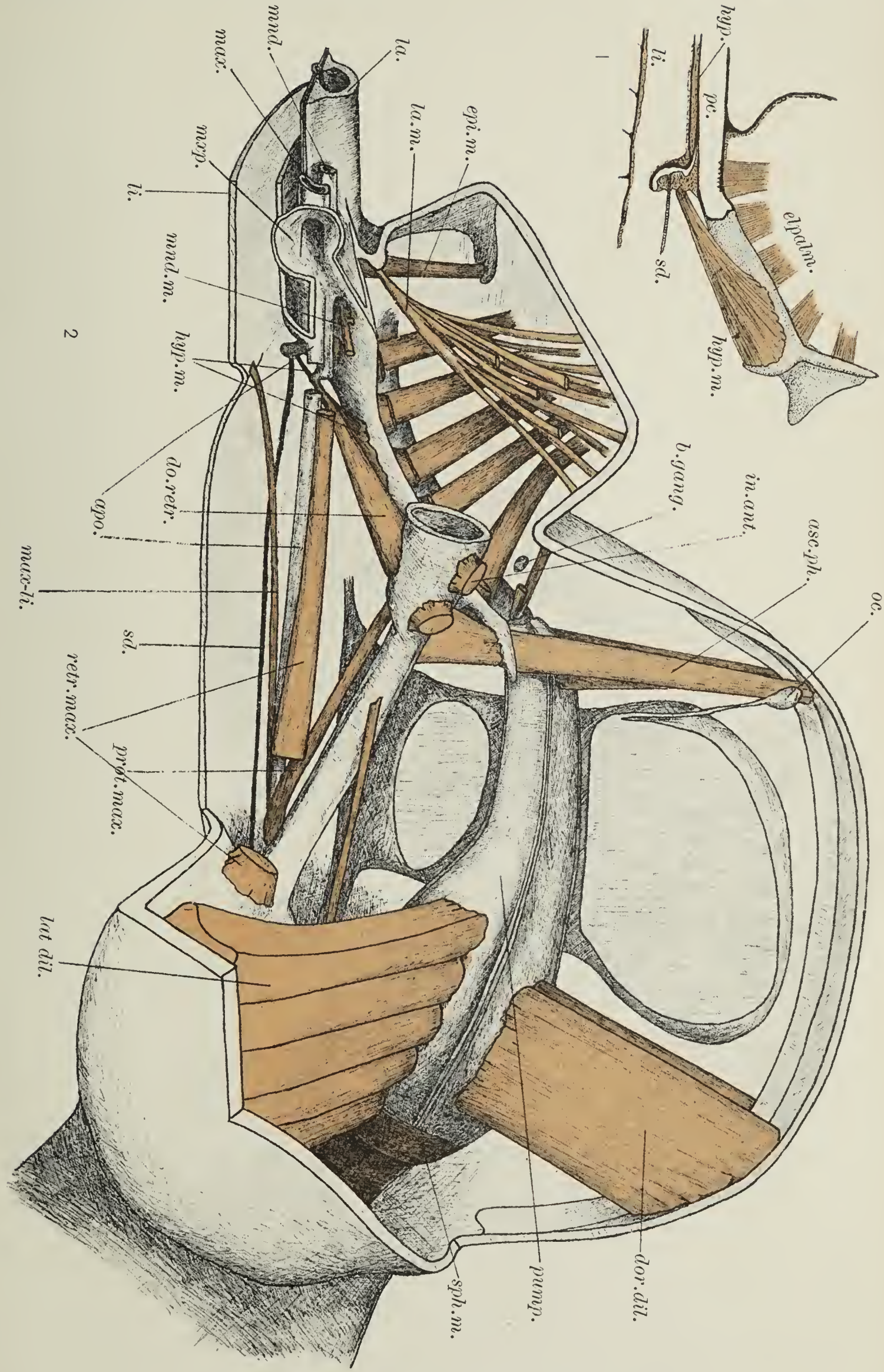

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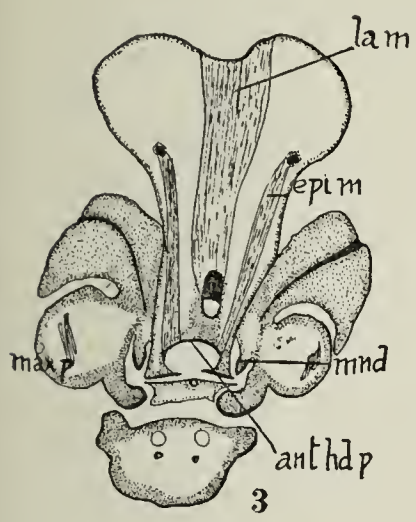
PLATE 13.

Figures 3–12 are sections of the head of a female Culex, each representing an actual section schematized; 3–6 and 9–11 are from one specimen, 7–8 from a second, and 12 is from a third. Figures 13–15 are similar schematized sections of the head of a female Anopheles. The figures are drawn to various scales. The median trachiole of the internal trachea is starred.

Fig. 3. Through bases of mandible and maxilla.
Fig. 4. Insertion of mandibular muscles; second section behind fig. 1.
Fig. 5. Salivary pump and insertion of maxillo-labial muscles; 9th section beyond fig. 1. Sections 10 μ in thickness.
Fig. 6. "Heads" of the tentoria and origins of mandibular muscles; 13th section beyond fig. 1.
Fig. 7. Through posterior spurs of pharynx and the pharyngeo-esophageal valve; specimen B.
Fig. 8. Anterior border of optic ganglion; specimen B.
Fig. 9. Midbrain section of specimen A.
Fig. 10. Origins of retractor maxillae muscles; 39th section beyond fig. 1.
Fig. 11. Through posterior ends of tentoria and insertions of protractors of the maxillae; 41st section beyond fig. 1. Specimen A.
Fig. 12. Region of bulbous portion of antlia; specimen C.
Fig. 13. Section of head of Anopheles; comparable in position to fig. 5.
Fig. 14. Section of head of Anopheles; comparable in position to fig. 11.
Fig. 15. Section of head of Anopheles; comparable in position to fig. 7.



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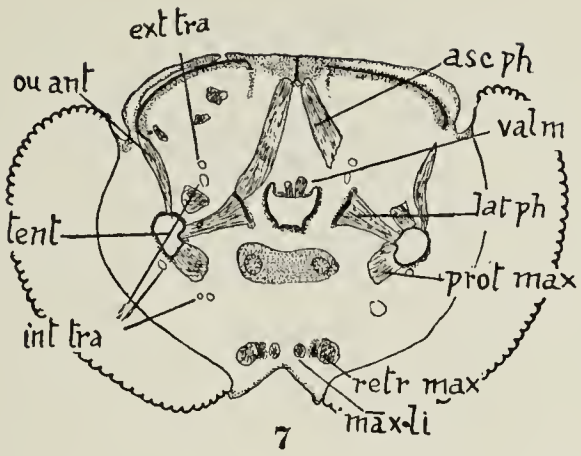

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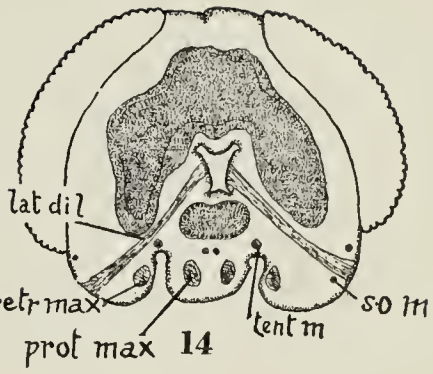

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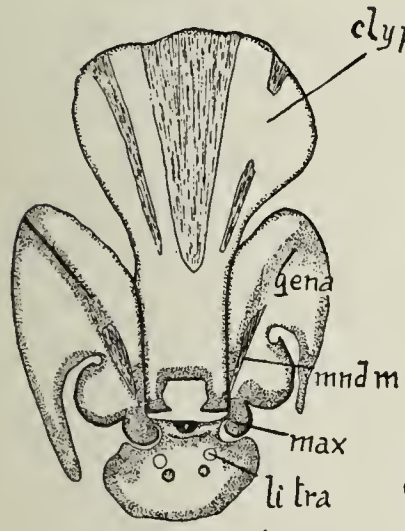

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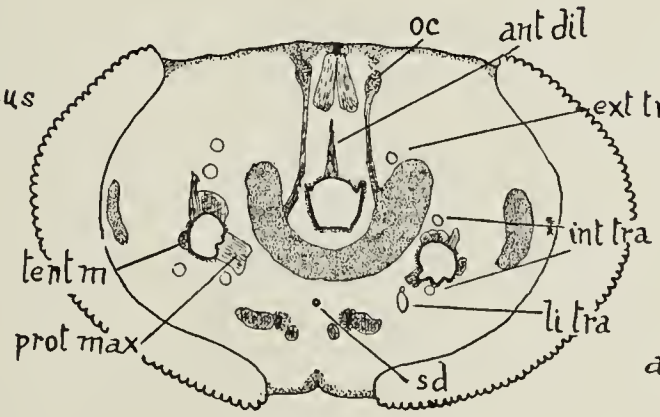

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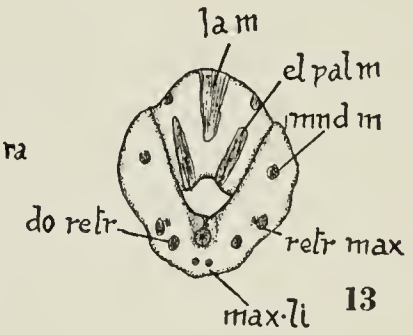

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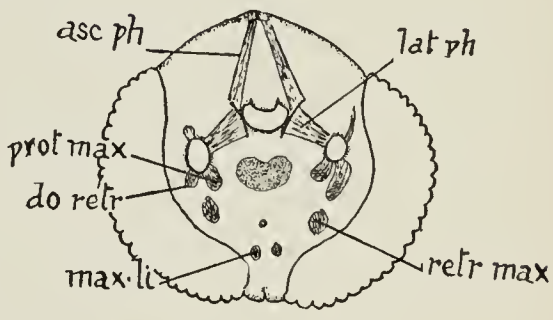

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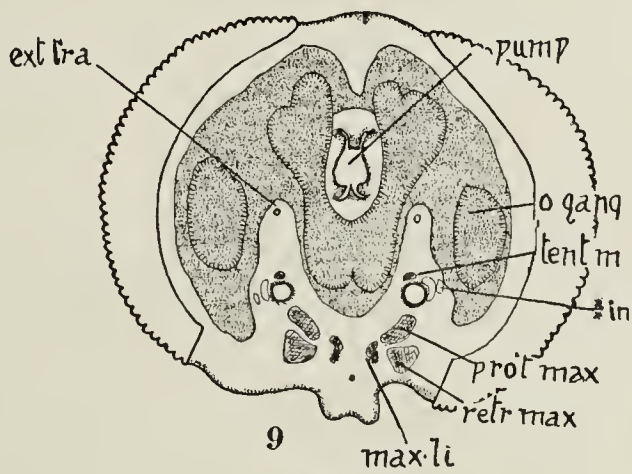

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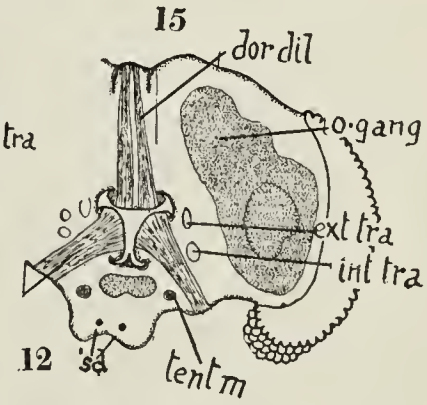

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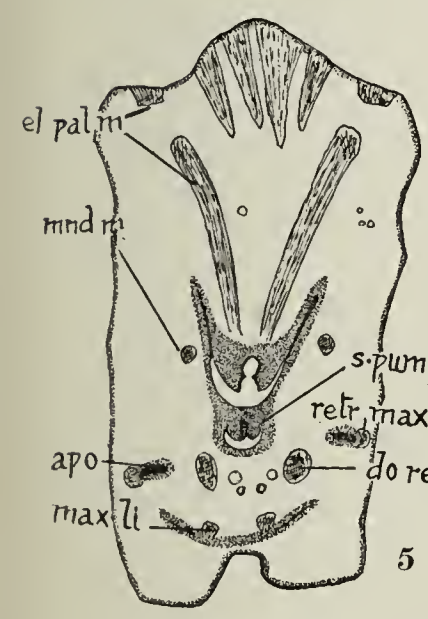

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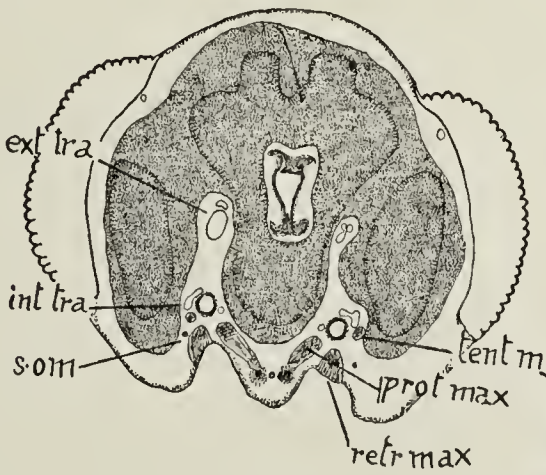

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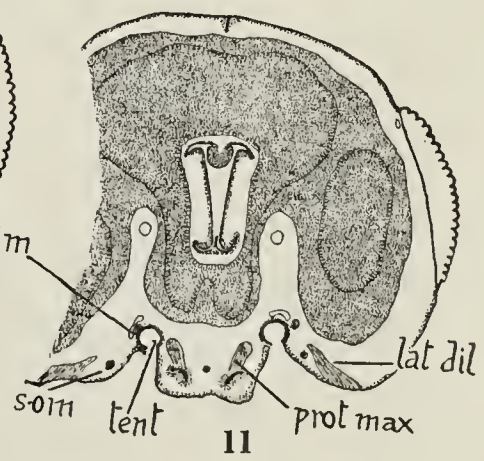

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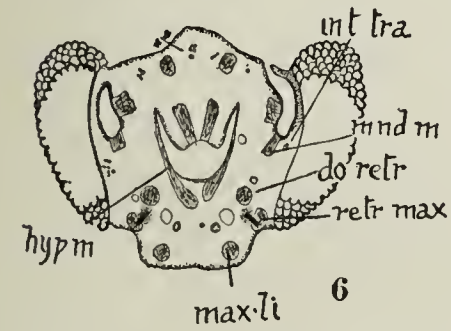

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PLATE 14.

Figures 16–19 represent various types of pumping apparatus in the Diptera.

Fig. 16. Section of head of Anthyomyia; monantlial type.
Fig. 17. Section of head of female mosquito; diantlial and post-neural type.
Fig. 18. Section of head of Tipulid fly; diantlial and amphineural type.
Fig. 19. Head of *Tabanus atratus*; diantlial and preneural type. (Free hand.)
Fig. 20. Alimentary canal of female mosquito with outline of body. (Free hand.)
Fig. 21. Longitudinal section through stomach and ileo-colon of female mosquito.
Fig. 22. Rectum of female mosquito.
Fig. 23. Salivary gland of a newly emerged imago of *Culex stimulans*. *ca* = central acinus.
Fig. 24. Mouthparts of a female pupa in which the hypopharynx (*hyp*) and proboscis canal (*pc*) are forming; transverse section.
Fig. 25. Hypopharynx and labium soon after the former is separated from the latter. Female pupa, transverse section.
Fig. 26. Alimentary canal of mosquito larva with outline of body. (Free hand.) *oes* = esophageal valve.
Fig. 27. Transverse section of wall of colon of a mosquito larva.
Fig. 28. Degenerating midintestinal epithelium of a pupa one hour old. *reg* = regenerative nuclei.

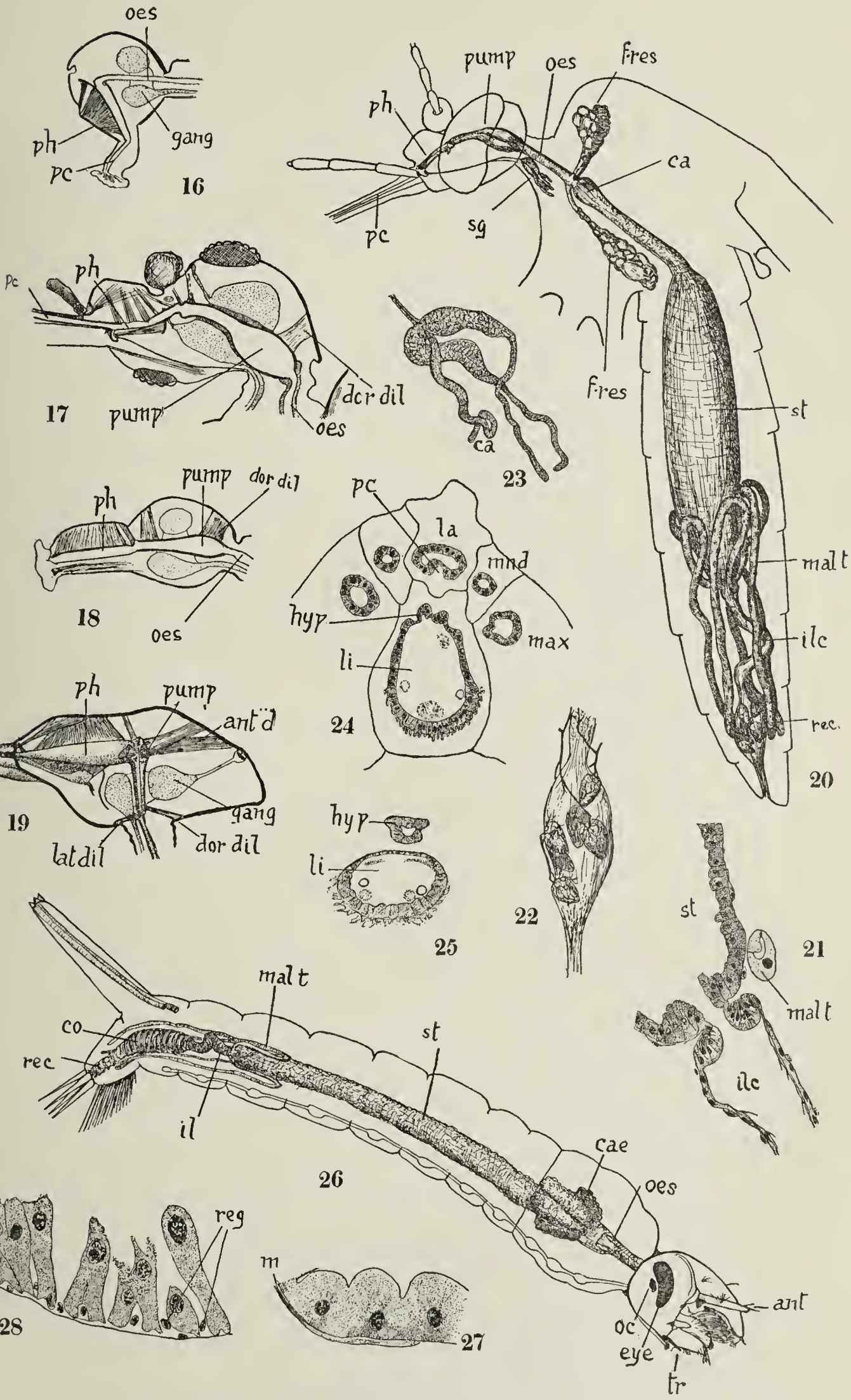
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PLATE 15.

Fig. 29. Semidiagrammatic view from the ventral aspect of the head of a mosquito larva ; picro-carmine preparation.

Fig. 30. Similar head from dorsal aspect ; younger specimen.

Fig. 31. Exuviated head cuticle to show relations of traverses, apodemes of the flabellae, pharynx, epipharynx, etc.

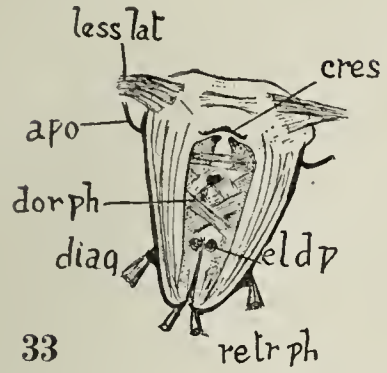
Fig. 32. Median longitudinal section of head of full grown larva ; compounded several sections. It is distorted so that the epipharynx lies too far back relatively to the labium and adjacent organs ; (compare with fig. 36) ; labial bud cut in midline between eminences.

Fig. 33. Dorsal view of pharynx of mosquito larva.

Fig. 34. Section of lower anterior region of head of mature larva to show relations of labial bud ; bud cut to one side of midline through one of the two eminences.

Fig. 35. Lateral aspect of larval pharynx, dorsal plate removed.

Fig. 36. Section of part of head of pupating larva to illustrate fate of ventral fold. *epi'* = cuticular sheath of epipharynx. Compare with figs. 32 and 34.



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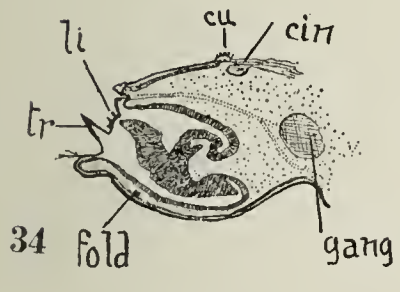

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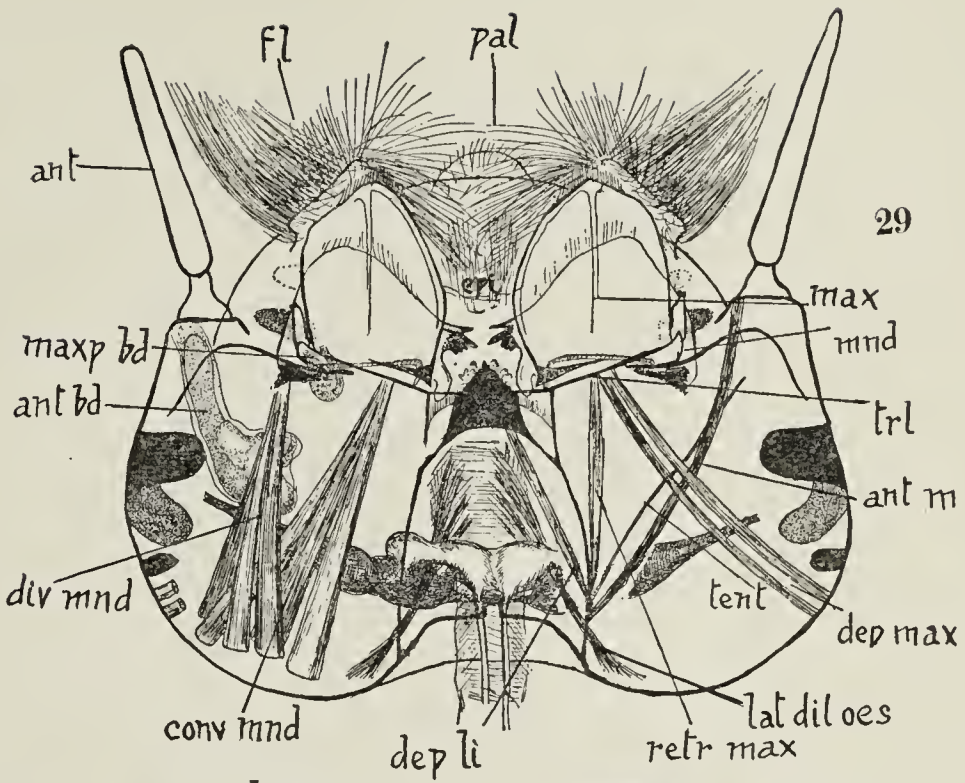

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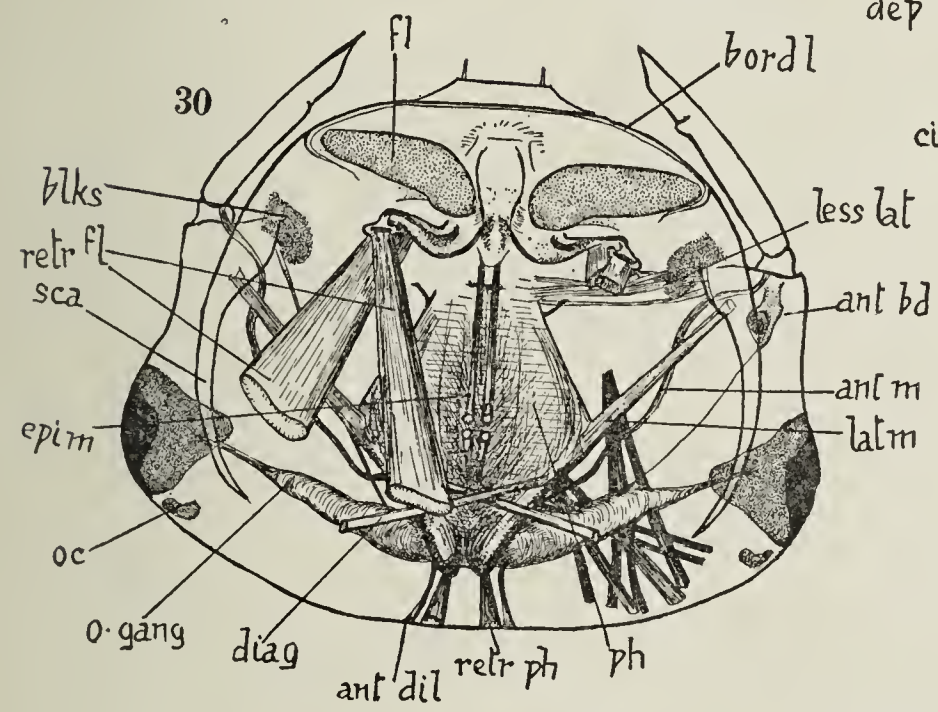

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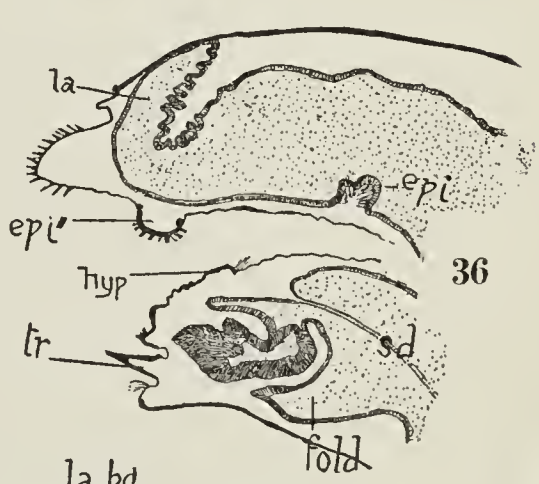

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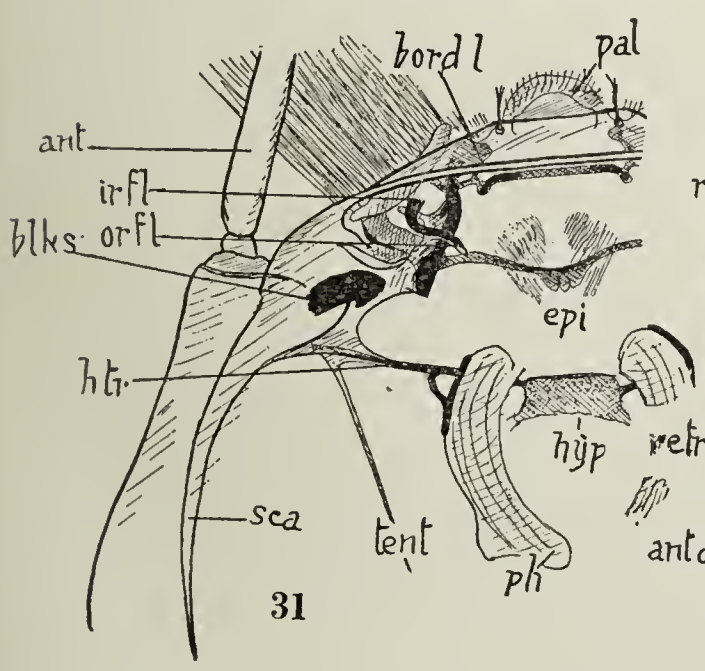

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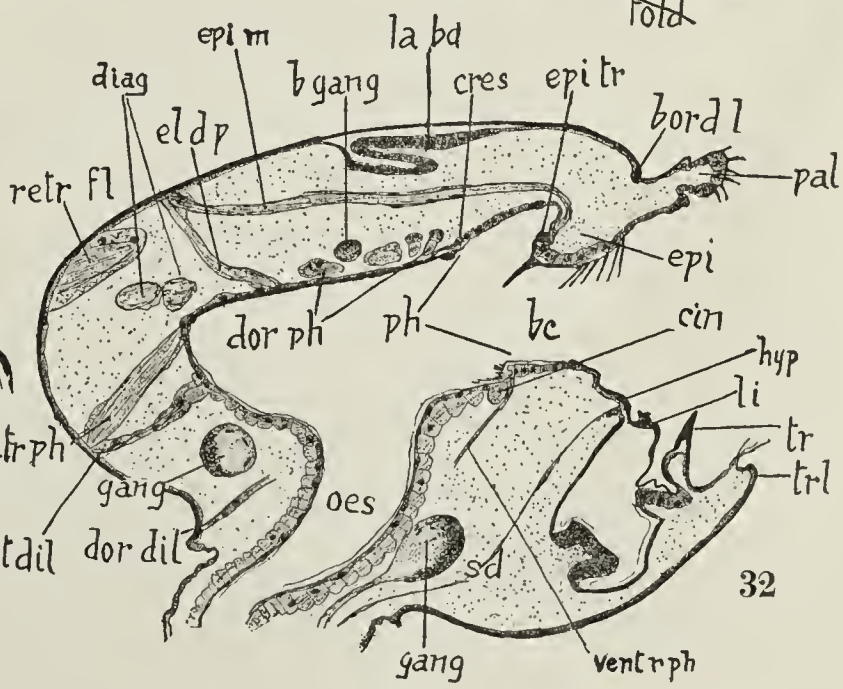

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PLATE 16.

Fig. 37. Esophageal valve and cardia of a full grown larva, striated border on cardia cells not distinct.

Fig. 38. Esophageal valve in a pupa four hours old; the left hand wall is ventral.

Fig. 39. Separation of the degenerated dermis of the epipharyngeal pit (*epi*) from the buccal cavity; longitudinal section of pupa ten hours old. Imaginal muscles (*x*) are beginning to form in the old masses of the retractors of the flabellae and epipharyngeal muscles and the hypopharyngeal muscles (*hyp m*) are forming at the base of the salivary duct.

Fig. 40. Esophageal valve of a pupa eleven hours old. The left hand wall is ventral. *f res* = ventral esophageal diverticulum.

Fig. 41. Esophageal valve of adult female mosquito; the right hand wall is ventral.

Fig. 42. Surface of ventral food reservoir or diverticulum of adult female showing the "striae" of the intima, a muscle fiber, and the nuclei of the epithelium. Bismark brown.

Fig. 43. Esophageal valve in a pupa ten hours old; the left hand wall is ventral. *v* = valve, *f res* = ventral diverticulum.

Fig. 44. Colon and rectum of a larva of the mosquito, longitudinal section.

Fig. 45. Portion of the wall of the stomach and ileum of a mosquito larva, showing ring of naked epithelium (*x*) at the junction of the two regions where the Malpighian tubules enter.

Fig. 46. Transverse section of mouthparts of male mosquito.

Fig. 47. Transverse section of mouthparts of female mosquito; level of tip of palps. The groove on the dorsal face of the labium in which the other stylets are received, has been obliterated by swelling during dehydration.

Fig. 48. Ventral aspect of head of Culex pupa at the moment that the larval head cuticle is ruptured. Dissected out and viewed as an opaque object. *fold* = fold in front of labial bud (*li*), see pl. 15, figs. 34 and 36.

Fig. 49. Side view of head of Culex pupa at moment when the respiratory trumpets free themselves by rupture of the thoracic cuticle; dissected out and viewed as an opaque object.

Fig. 50. Side view of the head of Culex pupa at a time just prior to the complete release of the mouthparts and legs from the larval cuticle. Their apices were still enclosed in the old sheaths. Dissected out and viewed as an opaque object. Drawn on a larger scale than the other figures.

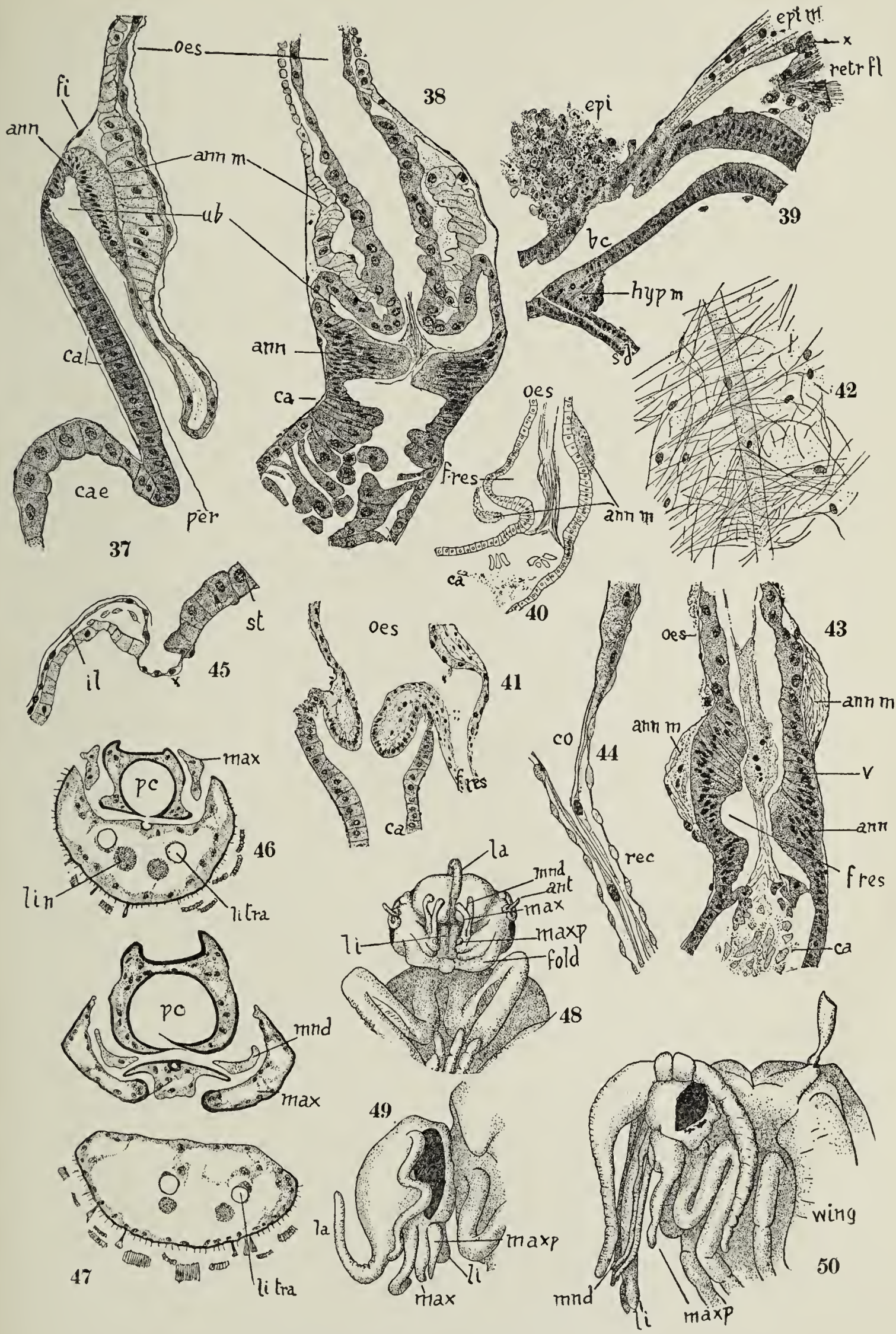
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PLATE 17.

Fig. 51. Ileum of pupa twelve hours old, showing the columnar character of the degenerating cells and some reconstructed epithelium (*reg*). *cir m* = circularis muscles.

Fig. 52. Colon and rectum in a pupa five hours old; temporary degeneration of the epithelium of the rectum. Owing to the collapsed walls many cells are cut tangentially and apparently lie in the lumen.

Fig. 53. Same region in a pupa twenty-one hours old, showing the beginnings of a rectal papilla (*p*) and the new-formed ileo-colon (*ilc*). Outside of this lie the remnants of the larval colon (*co*). A few of its muscles (*m*) are still recognizable.

Fig. 54. Diagrammatic longitudinal section of a pupa five hours old.

Fig. 55. Diagrammatic section of a pupa twenty-two hours old. The antlia is not yet formed. *f res* = ventral esophageal pouch.

Fig. 56. Outline of section of head of pupa four hours old. * = pharyngeo-buccal boundary.

Fig. 57. Outline of section of head of pupa seventeen hours old, epipharynx degenerated, muscles altering. * = pharyngeo-buccal boundary.

Fig. 58. Outline of section of head of pupa twenty-five hours old, the imaginal muscles and pump perfected. * = pharyngeo-buccal boundary, *val m* = *el d p*, *asc ph* = *retr ph* of figures 56, 57. *epi* = epipharyngeal muscles.

Fig. 59. Invasion of larval colon by cells of the ileum; longitudinal section of pupa seventeen hours old.

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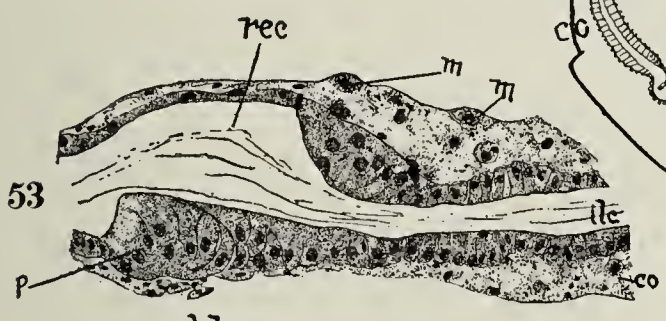

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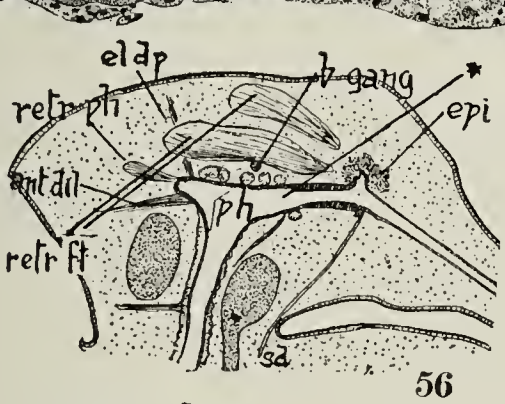

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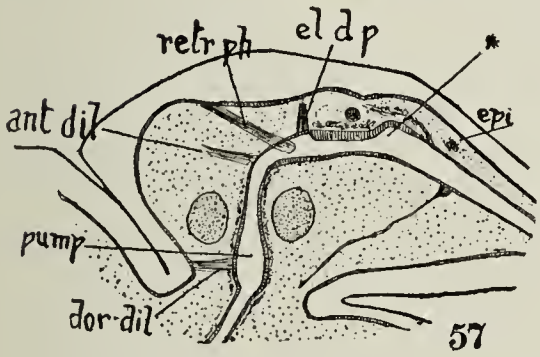

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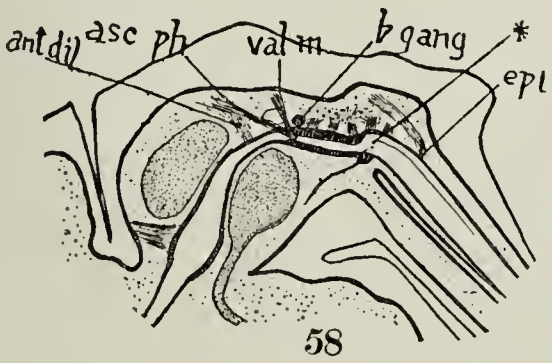

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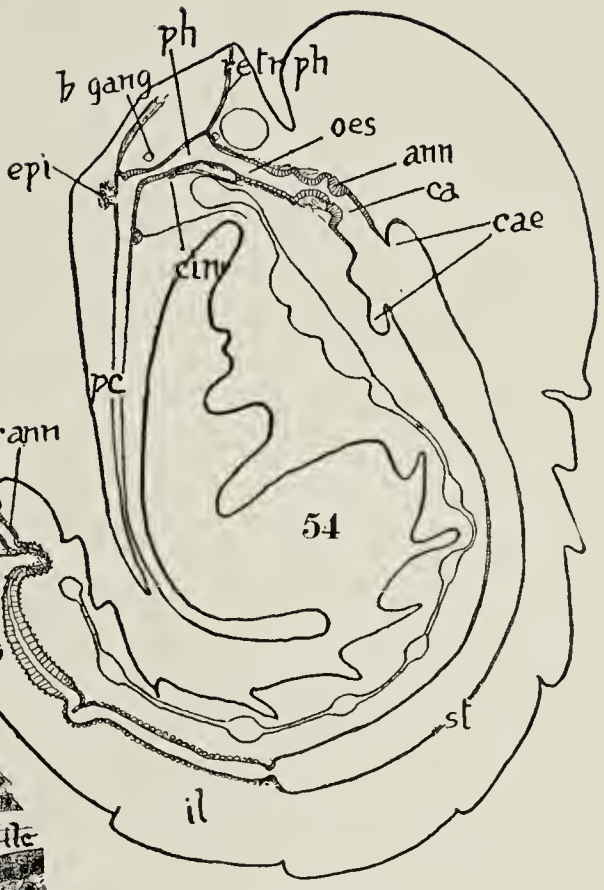

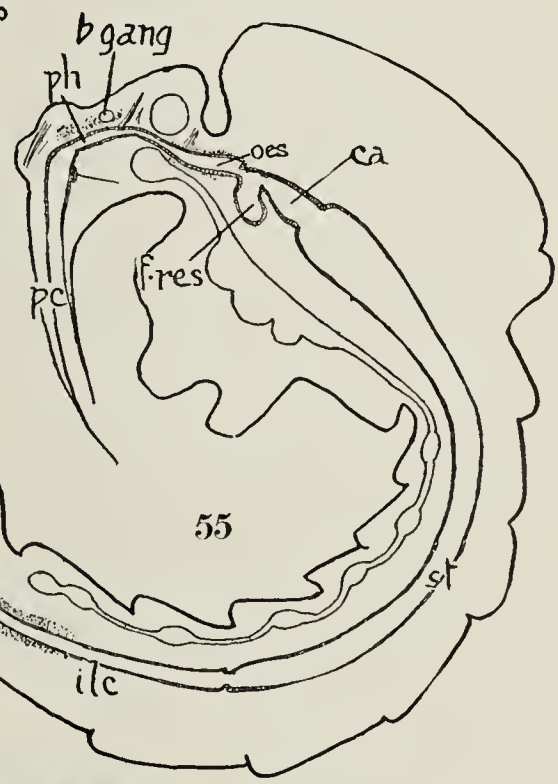

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p. 203–312.

BIRDS OF THE SOUTHERN LESSER ANTILLES.

By Austin H. Clark.

BOSTON:

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October, 1905.

No. 7.—BIRDS OF THE SOUTHERN LESSER ANTILLES.

BY AUSTIN H. CLARK.

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Introduction.

The specimens which, together with my field notes, serve as a basis for this list, were collected during a continuous residence in the Lesser Antilles from August 3, 1903, until September 22, 1904. I was on Barbados from August 3 to October 18, 1903, and again from January 2 to 16, 1904. On St. Vincent I remained from October 19, 1903, to April 10, 1904 (exclusive of two weeks spent on Barbados and a couple of short trips to the Grenadines) and again from July 2 to 11, and from September 14 to 21, 1904. I visited Bequia from November 30 to December 3, 1903, and from February 8 to 12, 1904, also calling in on my way to and from the other Grenadines. I spent December 9 to 11, 1903, on Mustique; March 23 and September 13, 1904, on Canouan; April 15 and part of March 24, April 26, and September 12 on Mayreau; April 24 and May 3 on Prune; March 25 to May 6, and September 5 to 11 on Union Island; July 29 on Petit Martinique; July 12 to September 5 on Carriacou; and from May 10 to June 30 on Grenada.

I had previously taken a few notes on the birds of the larger islands (Grenada, St. Vincent, and Barbados) during a trip through the West Indies from Trinidad to Bermuda, in 1901, when I spent August 9 in Grenada, August 10 in St. Vincent, and August 11 to 13 in Barbados.

The specimens collected during the trip are at present in the collection of Messrs. E. A. and O. Bangs, of Boston, Mass.

Literature.

Barbados.— The first account of the birds of Barbados is that of Ligon. His descriptions of the habits of the different species are bright and very interesting, but there is no attempt at classification, nor are all the species mentioned. Sir Hans Sloane touched at

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Barbados on his way to Jamaica, and includes some notes on the avifauna of the island in his narrative of the voyage and in his account of the natural history of Jamaica, making particular mention of sea birds, which he probably only met with off the coast (many species are abundant within sight of Barbados) inferring, from their abundance in the vicinity, that they inhabited the island. He also gives wild geese as visitors to the island (presumably in winter) although none of the other writers on the Lesser Antilles includes them, and there is but one record, a Brant shot in 1876. Hughes (**1750**) gives the first really good account of the birds of Barbados, his list being compiled from observations taken on the island during a residence in the northern part while rector of St. Lucy's parish. His descriptions (which are in many cases accompanied by measurements) are as a rule good enough to admit of satisfactory identification. It is a noteworthy fact that his notice of the breeding of *Puffinus lherminieri* in St. Lucy's, although apparently overlooked since his time, was proved to be correct through the researches of Col. H. W. Feilden almost 140 years later; and the truth of his assertions regarding *Vireosylva calidris barbadense* (giving it as an inhabitant of the Scotland district) I was enabled to confirm 154 years after his date of writing. Sir Robert H. Schomburgk (**'48**) included a list of the birds in his history of the island, which, although not so carefully prepared as that of Hughes, contains some interesting features, being the first list adopting the binomial system of nomenclature, and recording the first capture of a Ruff (*Pavoncella pugnax*) on the American side of the Atlantic. Between 1848 and 1889 there were many short notices published dealing with certain of the birds of the island, and in the latter year Col. Feilden prepared an article on the ornithology of Barbados, containing the results of his observations and a summary of previous lists, prefaced by a description of the geology and faunal characteristics of the island. This is the best account that has appeared dealing with the avifauna of any one of the Lesser Antilles.

St. Vincent.— There have been three lists published on the birds of St. Vincent, besides a few notices on certain species inhabiting that island. The first general catalogue is that of Lawrence, which includes the field notes of Ober, taken while collecting in St. Vincent; the second, which is in some ways superior, is by

Lister, who resided for some time in the island, and was thoroughly acquainted with its ornithology. The latest list is by the present author, and is of practically no scientific importance, having been compiled from memory during a stay there for the West Indian bulletin, at the instance of Sir Daniel Morris. It was written more as a guide to protective legislation than as an enumeration of the species inhabiting the island, and is, unfortunately, replete with editorial and typographical errors. The preface, including an account of the geology of St. Vincent, is, however, useful.

The Grenadines and Grenada.— Wells' articles on the ornithology of Carriacou are (except for a few passing notices by the earlier authors, and a short note by Lawrence) the only references we have to bird life in the Grenadines, and the present author has been the first to undertake a thorough investigation of those islands. It is to be regretted that nothing has hitherto been written concerning this district, where the South American and West Indian forms are more or less intermixed, as otherwise we should have at our command much valuable information regarding the encroachment of the continental element upon Lesser Antillean territory, a considerable part of which appears to have taken place in very recent years. Four lists of the birds inhabiting Grenada have been published in addition to a number of articles that mention certain species of that island or describe new forms. The first was by Lawrence ('78b) based on the notes and collections of Ober. Six years later, John Grant Wells, a native of Grenada, published at St. George's a small pamphlet containing the names of the birds of Grenada, as identified by Lawrence. This was followed in the same year by an excellent account of the avifauna of the island written by Wells, and prepared for publication by Lawrence. In recent years there has appeared in each issue of the Grenada handbook a list of the names, both scientific and local, of all the birds known from Grenada, and another of the birds found at Carriacou. The former was compiled by Wells for the Handbook, and the latter was taken from his articles on the birds of Carriacou.

The appended bibliography contains the more important references to the literature on the ornithology of the southern Lesser Antilles, and the works of the earlier authors who have dealt with this group of islands in general. Monographs of certain groups, books dealing with North, Central, or South American species, or

with the birds of the world which include notices of species herein mentioned, are omitted; but the references to them may be readily found by consulting the bibliography and the authors listed under each species in Cory ('89, '92), in Ridgway's Birds of North and Middle America, and in the Catalogue of birds in the British museum.

Geology and Geography.

Barbados. — Barbados, although not separated from the main Antillean chain or from South America by any great expanse of water (the nearest islands, St. Vincent and St. Lucia, being only about one hundred miles away), can lay claim to being truly oceanic in the sense that it has never formed part of a continent since the introduction of its present comparatively meager fauna.

The strata which form the basement series of Barbados are extremely contorted, and have been greatly disturbed. They consist of silicious sandstones, calcareous sandstones, clays containing selenite, clays impregnated with mineral oils, and, at some points, bituminous coal. Their precise age has not yet been determined, but they are probably late Eocene or Miocene, and point to a correlation with those of Trinidad, and, consequently, at one period to a connection with the South American continent. These strata, over about six sevenths of the superficial area of the island, or about ninety-one thousand acres, are covered with a capping of coral rock, while the area from which the coral has been denuded by sub-aerial causes, and where the basement rocks are exposed, occupies only about sixteen thousand acres, locally known as the "Scotland district" because of its peaked and hilly character. It is in this part of the island that the highest altitudes are reached — Mt. Hillaby, 1104 feet, Mt. Misery, 1053 feet, and Hackleton's Cliff, 997 feet, among others. The rest of the island is low and rather flat, or at most gently rolling, thus offering a great contrast to the Scotland district, which is a part of the island that the average tourist never sees. It can hardly be doubted that these basement rocks (or Scotland series) were formed either as estuarine or shallow sea deposits, and in close contiguity with some great land area. Resting unconformably upon the Scotland series are vast deposits of oceanic ooze, built up, in some cases almost entirely, from the tests of rhizopods.

The modern coral cap of the island has been built up step by step on these thalassic oozes as they emerged from the ocean.

The present island of Barbados dates back no further than the period when the process of upheaval brought the deep-sea deposits sufficiently near the surface to admit of the reef-builders commencing work. The deep water which surrounds Barbados (soundings of 1000 to 1500 fathoms being shown on the charts between it and the Antillean chain, and of over 1000 between it and Tobago to the southward) is proof that it has had no continental connection since it emerged as a reef from the ocean.

Barbados is situated in latitude 13° 4′ N., and longitude 59° 37′ W., and is the most easterly of the Antilles. It is about 21 miles long by 14 broad, with an area of 166 square miles, being about the size of the Isle of Wight. The population is nearly 200,000. The chief town is Bridgetown, on Carlisle Bay, near the southwestern extremity; the next in importance is Speightstown, in St. Peter's parish, towards the north, with the remaining town, Holetown, situated between them in St. James. The island is almost entirely under sugar cane, there being but a few small bits of woodland, remnants of the forests with which it was covered at the time of its discovery. The rainfall is said to be about 60 inches, the rain usually coming in the shape of transient showers. The dry season occurs in the winter and early spring months.

St. Vincent.— The geological formation of St. Vincent is purely volcanic, and all the rocks on the island indicate that origin. A central backbone of mountainous country (not a single ridge, as shown on many maps) varying in height from 2000 to 4000 feet and densely wooded, traverses the island from north to south. At the northern end of this ridge is the highest peak on the island, the Soufrière; next to it is the Morne Garou with an altitude of over 4000 feet, while at the southern extremity is Mt. St. Andrew, 2500 feet, overlooking the Kingstown valley. Rocky and wooded spurs run down to the sea along the western or leeward coast, ending abruptly in high rocky cliffs, that alternate with small sandy beaches at the ends of the valleys. The windward side of the island, especially toward the north, is a broad and fertile tract that slopes gently back from the sea for a distance of some four miles to the base of the hills of the central mountain range. It is known locally as the Carib country from having been, upwards of a century ago, allotted to the aborigines for their occupation.

All the valleys are fertile and well watered with streams of good water, whose origin is high up in the mountains. These streams in the dry season are comparatively small, but swell into raging torrents after heavy rains. The windward slopes of the Soufrière and vicinity are drained by the Dry River. The channel of this river, a stream of average size before the eruption of 1812, was at that time completely filled and choked with scoriae, rocks, and gravel underneath which the water now ordinarily finds its way to the sea, disappearing some distance before it reaches the coast. In floods, however, the water comes down with great force and in large quantities, filling the rocky bed, which is 200 yards across at the point where the windward road crosses it. On these occasions it is very destructive, and has already washed away many acres of cane land on its right bank.

The slopes of the higher mountains are scored with deep ravines, and during the rainy season white clouds hover over them day and night. Here the vegetation partakes largely of an arboreal character, with an abundant undergrowth of ferns, and, on the margins and banks of streams, species of Scitaminae, Aroideae, Cyperaceae, and some palms. Of the true ferns there are four species of Cyathea, two of Hemitelia, and three of Alsophila. At all elevations on the mountain slopes are numerous open glades, showing the sites of former cultivations that have become covered with coarse grasses and dry-loving ferns, such as Gleichenia.

In the lowlands, in valleys, and on easy slopes, the original vegetation has been for the most part cleared off, and in its place are fields of arrowroot, sugar cane, and other plants. On the rocky cliffs are found numerous trees and bushes of stunted growth, some of them overhanging the sea.

St. Vincent (like Barbados) is singularly free from swamps; hence there is nowhere any large extent of that tangled vegetation so characteristic of marshy districts in the tropics. The mangrove trees are only very sparsely distributed. The manchioneel (*Hippomane mancinella*) and the seaside grape (*Coccoloba uvifera*) are found on the sea beaches in the Windward district.

The island of St. Vincent is situated 98 miles directly west of Barbados, and 21 miles south-southwest of St. Lucia. It is 18 miles in length by 11 in breadth, with an area of 132 square miles, and a population of about 40,000. The chief town is Kingstown,

in the southwestern part; next in importance comes Georgetown, on the windward coast near the Soufrière. The other towns are Chateaubelair, near the base of the Soufrière on the leeward coast, Barrouallie, about halfway between Chateaubelair and Kingstown, Layou, between Kingstown and Barrouallie, and Calliaqua, three miles southeast of Kingstown. The rainfall is roughly 100 inches, but varies greatly in different parts of the island, being considerably more in the mountains.

The Grenadines.— The island of Bequia, the largest of the Grenadines except Carriacou, and the most northerly of the group, lies about 9 miles south of St. Vincent. It is of irregular shape, long and narrow, running from northeast to southwest. It is about 6 miles in length, with an area of 6 square miles and a population of about 2000. Near the southwestern end is the town, situated on a fine natural harbor, Admiralty Bay. A large part of this island is low and almost flat, or gently rolling, and presents a strong contrast to St. Vincent, but there is some rugged land toward the northwest, where the island ends abruptly in a tall cliff known as Bequia Head. There are some moderate elevations behind the town toward the windward coast. There are no swamps on the island, but small patches of mangroves are found along the beaches on the windward coast, especially on the seafront of the Spring estate. There are also many manchioneel trees along these beaches. The island is now largely given up to pastures in the flatter districts, the beautiful Spring estate with Industry just beyond and Union near the town being the most extensive of these. The hilly parts of the island are covered mostly by woods, which, however, are not so luxuriant as are those on St. Vincent, since the rainfall is only about half as much. There are no ponds nor streams on the island.

Off the shores of Bequia are a number of small keys, the majority of them thickly covered with scrubby vegetation. The most important of these are Petit Nevis and Isle à Quatre to the southward, and Western Key, just south of the entrance to the harbor.

Père Labat (**1722**, p. 220) states that in his time Bequia contained dangerous snakes, and was for that reason known as "Petit Martinique," though, as he says, it might just as well have been called "Petite Sainte-Lucie."

Battowia, about 9 miles southeast of Bequia, is little more than a large rock, thickly covered with stunted vegetation. The sides are

precipitous, and the cliffs about the island serve as breeding places for many sea birds, chiefly boobies (Sula).

Half a mile southwest of Battowia lies Balliceaux. It is a little larger than Battowia but less rugged and contains a considerable amount of cleared pasture land.

South of Bequia and southwest of Balliceaux lies Mustique, the prettiest of all these little islands. The land is gently rolling or nearly flat, and is largely cleared for the pasturing of horses and cattle. In a belt across the middle of the island and toward its eastern end the trees have been allowed to remain. The woodland is of the same character as that on Bequia — strangely free from underbrush for tropical growth. Near the northern shore there is a large pond with a wide border of mangroves, and near the eastern end there is a quiet, almost landlocked, mangrove-lined bay. Along the northern coast there is a fringe of manchioneel and other large spreading trees, of varying width, just such a growth as is preferred above all others by the Seaside Dove (*Zenaida zenaida aurita*), which is consequently very common here. Taken all together, Mustique puts one strongly in mind of a well laid out northern park, with its bits of woodland, ponds, fences, and so forth. There are about 60 people on the island, including Mr. Charles Wallace, the manager, and tenants of the Hazell family of St. Vincent, to whom the island belongs.

There are many small islets and keys about Mustique, to the north being, among others, the three rocks known as the Pillories, upon which are usually to be seen many sea birds, chiefly pelicans and boobies; to the southwest, Petit Mustique, and, farther still, Savan and Petit Canouan.

The island of Canouan, southwestward of Bequia and Mustique, is separated from them by a long stretch of open sea, broken only by the little keys just mentioned. It has, according to Edwards (Hist. West Indies, vol. 1, p. 405) an area of 1777 acres, or about 2.8 square miles. It is in general rugged and hilly, but there is some flat land near the southern extremity. Almost the whole of Canouan is covered with rough scrubby growth, exceedingly difficult to penetrate. There are no pastures to speak of, and no high woods. The main town is toward the center of the island, about a mile from the bay (which is in the southwestern part) and near a large, almost landlocked cove, locally known as the "Canash." The

residence of Mr. Henry Snagg, the principal owner of the island, is here, and near it is a little stone chapel in which breeds a colony of martins (*Progne dominicensis*). There is a small collection of houses near the shipping bay, mostly of "wattle and daub." The population of Canouan is stated to be about 400.

Mayreau, or Mayero, lies a few miles southwest of Canouan. It is a small island, with almost no trees except a few manchioneels on the beaches, and is bare and windswept. It is mostly given up to the cultivation of "Marie Galante" cotton, and (in the spring) Indian corn. There is a small amount of scrubby growth on a hill to the northeast of the town. All the houses on Mayreau are near the top of a fairly high hill, about half a mile from the southern shore. The walk up to the town from the beach is very tiresome — a continuous climb without the slightest shelter from the heat of the sun. The chief house of the island, the residence of Miss Jane R. St. Hilaire, the principal owner, is pleasantly situated on the summit of the hill just mentioned, and commands a splendid view of Union Island, Carriacou, and Grenada to the south, and of the northern Grenadines and St. Vincent to the north.

There are a number of small keys about Mayreau, the most important being the Tobago Keys or Four Sisters, just to the southeast, a group of four small islands all much alike and very near together, each a rounded hill with a small bit of flat land, covered with scrubby trees, bushes, and cactus, a detestible plant known locally as "nettle" (but much more to be dreaded than the plant to which we give that name), and in the flat places, with "burr grass." There is a very small sand bar just southwest of these islands, on which may usually be seen a few terns (*Sterna maxima* and *S. dougalli gracilis*) and gulls (*Larus atricilla*). A large solitary rock 203 feet high known as Sail Rock rises from the sea several miles to the eastward of Mayreau, and is the home of many sea birds.

South of Mayreau and just halfway between Bequia and Grenada is Union Island, with an area (according to Edwards) of 2150 acres or about 3.2 square miles. This island is high and rugged, particularly in the western half; but toward the eastern end there is a considerable area of flat land at the base of the hills, especially on the northern side, where they slope more or less gradually toward the sea. There is a gap in the central backbone, through which a bridle path passes from one coast to the other, with a mod-

erately steep slope up to the hills on the east side. Toward the west is a fairly level valley extending in for half a mile or so when it suddenly rises to a high grassy plateau used for pasturing stock, and locally called the "Savanna." This gap is dominated on each side by a high mountain, the one on the western side being very steep and having an altitude of 1010 feet. The chief town of the island, Ashton, is situated at its base. The principal house of the island, the home of former owners, is a large brick structure on a hill at the southeastern extremity of the island, about two miles from Ashton. Near it is a collection of about a hundred wattle-and-daub houses, comprising the village of Clifton. The rough land about the base of the hills is put under cotton and corn, and the flat land under pigeon peas and sweet potatoes. The population is estimated at a little over 2000.

Just east of Union Island lies the small island of Prune. This key is mainly flat and swampy, but has two steep hills, one in the northeast, and the other in the southwest corner. The vegetation is mainly tall scrub and stunted trees, with numerous mangroves, especially in the northern part. This island is remarkable as being the only place where *Dendroica ruficapilla* occurs in abundance in the Lesser Antilles, south of Dominica.

Near the town of Ashton is Frigate Rock, a tall rocky hill rising abruptly from the sea.

The island of Carriacou, the largest and most important of the Grenadines, lies about eight miles south of Union Island, and twenty miles north of Grenada. It has an area of about 13 square miles. In the center of the island is a ridge, running from north to south, of fairly uniform height, with two peaks of considerable elevation, High North (980 feet), and Chapeau Carré (960 feet) at its southern end. A number of spurs run out from this ridge to the sea on either side, between which are remarkably level valleys extending in for some distance from the coast, and then rising rather abruptly to the central ridge. In many of these valleys, notably at Harvey Vale on the southern shore, near the town of Hillsboro' on the west, and at Lauriston halfway between, there are extensive swamps. On the ridges and on many of the hillsides there is a large amount of scrubby growth and stunted trees; but on the gentler slopes and in the valleys the land is mostly taken up with the cultivation of "Marie Galante" cotton and Indian corn, as

on the neighboring islands. In the flatter areas, particularly at Dumfries on the east, Harvey Vale on the south, and Beausejour near Hillsboro', there is a considerable area of flat pasture land. The hills have been very largely denuded of trees for the purpose of building peculiar craft of from five to fifty tons burden known locally as sloops and schooners. There are some rocky cliffs on the southern end of the island, and off the southeastern, southern, and southwestern shores lie the small islets known as Frigate Island, Saline, White, and Sandy Islands, Isle de Large, Mabouya, and Jaques Adam. These are mostly small wooded hills rising out of the sea, with a bit of flat land about their bases. Some are mere rocks. Carriacou, like all the Grenadines, is very dry, having a rainfall of only about 50 inches, or less than half that of St. Vincent and Grenada, and no running water. The population is about 7000.

Petit Martinique (so called because the French who discovered it found snakes there which they considered similar to those on Martinique) lies a few miles to the northeast of Carriacou. It is merely a conical hill, sloping down evenly to the sea on all sides, with a small strip of comparatively level land about the base. The vegetation resembles that of Carriacou. Between it and Carriacou lies Little Tobago, a small island, thickly covered with scrub (mainly thorn bushes) and cactus. Just to the north lies Little St. Vincent, simply a moderate sized hill rising out of the sea. Petit Martinique has a population of 350, and Little St. Vincent, 20.

Between Carriacou and Grenada is a long string of rocks and islets, of various shapes and sizes, the most important being Isle Ronde and Les Tantes. About halfway to Grenada is a high and precipitous rock known as "Kick-'em-Jenny," formerly a leper settlement, but long since uninhabited. It forms the home of hundreds of sea birds, mainly boobies (Sula).

Carriacou appears to be, in the main, composed of beds of fine-grained volcanic sands and tuffs. On the eastern slopes of the island, and at Belair (in the center), at an altitude of 600 feet, the tuffs of which the hills are composed, are covered with layers of a shallow-water foraminiferal limestone, from ten to twenty inches in thickness. It therefore appears to consist of layers of volcanic ash which were deposited in the sea, and afterwards covered with the shallow-water deposit. Later this was subjected to upheaval, with

the result that part of the limestone was raised to at least 600 feet above sea level. The rest of the Grenadines are geologically much like Carriacou, but appear to lack the limestone capping of that island.

Grenada.— Grenada is situated in latitude 12° 3′ N. and longitude 61° 45′ W., and is approximately 90 miles north of Trinidad, 68 miles south-southwest of St. Vincent, 60 miles northwest of Tobago, and 100 miles southwest of Barbados. It is the most southerly of the true West Indian islands, as Tobago and Trinidad are faunally and geologically a part of South America. It is about 21 miles long by 12 miles in greatest breadth, and has an area of about 120 square miles. In shape it is an irregular oblong, lying north and south, broader at its southern than its northern extremity, with a central backbone of mountainous country running through its whole length, somewhat closer to its western than to its eastern seaboard. The highest altitudes are Mt. St. Catherine (2749 feet), Mt. Sinai (2300 feet), and the mountain overlooking the Grand Etang (2014 feet). Along the eastern and southern coasts the mountains slope gradually to the sea, so that the land is therefore undulatory and fairly level; but on the western side the mountains fall more or less abruptly, and give the coast a rugged and picturesque appearance. The higher portions of the slopes are wooded, while the lower slopes are given up to the raising of cocoa and nutmegs, with occasional cane-fields. In the vicinity of Grand Anse and Point Saline at the southern extremity of the island, where the rainfall is comparatively small, there is a large amount of scrubby growth, with a considerable area under pastures. This part of the island is strikingly different from the remainder, and brings forcibly to mind the conditions existing on the Grenadines. There are a number of small wooded islets and numerous rocks along the eastern and southern shores. The chief town, St. George's, is situated on an excellent natural harbor in the southwestern part of the island. Next in importance comes Grenville or Labaye, on the windward coast, in the parish of St. Andrews. The other towns are Sauteurs, on the northern end in St. Patrick's parish, and Gouyave and Victoria between Sauteurs and St. George's on the leeward (western) coast. The population of Grenada is about 70,000.

Grenada, like St. Vincent, is volcanic, but is apparently of greater age than the majority of the Lesser Antilles. Below from 700 to

800 feet, the valleys are principally cut in beds of volcanic conglomerate, tuffs and ashes, frequently intersected by dikes of basalt and andesite lavas. At elevations above 700 feet beds of conglomerate and tuffs are far less common, and the hillsides consist chiefly of disintegrated lavas of various kinds, the fragmental materials of which have doubtless been removed by the great amount of denudation that the rocks have undergone. Partially decomposed lavas possessing to some degree the properties of pozzuolano are of frequent occurrence, and are locally termed "tiff." In the extreme north of the island are some raised limestone beaches.

Politically, Barbados is a colony by itself, having no connection with the other British West Indies. Grenada, St. Vincent, and St. Lucia form what is known as the colony of the Windward Islands, with the seat of government at Grenada. St. Vincent includes not only the island of that name, but also all the Grenadines north of Carriacou. The southern part of Petit Martinique, Carriacou, and the islets to the south are governed from Grenada.

Meteorological and Geological Phenomena.

Barbados has, in the course of its history, been visited by a number of hurricanes of varying severity. The last notable one occurred in September, 1898, and laid a large part of the island in ruins. The destruction of avian life was very great. Hundreds of birds were killed outright in the woods and fields, and many more were blown off into the sea and drowned. The decrease of some of the species, as for instance the blackbird (*Holoquiscalus fortirostris*) was at the time very marked, but they have all now nearly regained their former status.

On September 11, 1898, St. Vincent experienced one of the most destructive hurricanes that has ever occurred in the West Indies. The center of the storm passed directly over the island, and the interior forests as well as the fruit trees on the cultivated areas were almost entirely destroyed. On the next day the island appeared as if it had been swept by fire; there was not a leaf nor any green thing in sight. Everything was brown. The number of birds was very sensibly diminished, those of the "high woods," especially the parrots (*Amazona guildingii*), appearing to have suf-

fered the most. Hundreds, if not thousands of birds were killed on the island, and quantities were driven out to sea and lost. *Allenia albiventris* after the storm became a common resident on Union Island and Carriacou (possibly on some of the other Grenadines also), places where previously it had been unknown. It has since, however, died out at both places. One or two parrots (*A. guildingii*) were picked up dead on the shores of St. Lucia. The effects of the storm were not felt all at once. For days afterwards parrots and "Ramier" (*Columba squamosa*) would stray into the smaller towns in so helpless a condition that many fell a prey to the negroes. It is possible that starvation was the cause of this, as every green thing had been destroyed, and it was several days before the trees began to put forth buds. When the vegetation did begin to recover from the shock the whole island, I was told, presented much the appearance of a rugged New England landscape in the spring. A number of the parrots were obtained alive at this time, and some of them are living in captivity yet. Several were sent to England, where, I believe, one or two are now in the Zoological society's garden at Regent's Park, and Messrs. T. R. Nairn and Thomas Osment of Kingstown have each a beautiful bird in their possession.

Bequia was also considerably damaged by this storm, but the other Grenadines escaped; there was a strong gale at Canouan, and a moderate one at Union Island, but only slight damage was done at the former place and none at all at the latter.

On May 7, 1902, occurred the first of the late eruptions of the St. Vincent Soufrière, which resulted in the loss of almost 2000 lives and the total destruction of every living thing on and in the vicinity of the volcano. The whole district was buried under tons of "ash" and scoria. The devastated area was about one third of the entire island and was the district from which the types of *Myadestes sibilans* and *Catharopeza bishopi* had been obtained; it was on the Soufrière, actually within the crater, where formerly the latter of these two birds had been most frequently met with, and the higher altitudes of that mountain were the chosen home of those exclusively woodland species which inhabited the island. The ejecta from the volcano fell with sufficient force at Belair estate at the opposite end of the island (fourteen miles away) to riddle the leaves of the breadfruit trees and, without doubt, to kill such small

birds as had not taken refuge under cover. After the eruption the whole island looked as if it were covered with gray snow. This possibly resulted in the death from starvation of many of such species as are habitually ground feeders (*e. g.*, *Geotrygon montana*). The ash fell in great quantities on Bequia and on Mustique, but appears not to have done any damage, at least as far as the avifauna is concerned. Further eruptions occurred on September 3 and October 15, 1902, and on March 22, 1903, but probably their effect was very slight as compared with the great havoc wrought by the outburst of May 7.

Neither Grenada nor the Grenadines (with the exception of Bequia) have ever experienced a storm severe enough to have seriously affected their bird life.

Present Status of Bird Life.

In the West Indies, as Taylor says (Ibis, 1864, p. 157), birds are not nearly so abundant as in northern countries. In the islands under consideration, they are much commoner on Grenada than anywhere else, doubtless because of the fact that this island is outside of the hurricane belt. The Grenadines are well stocked with birds (although the number of species is limited), but they are not very plentiful in Barbados, while there is hardly a species which may be called common on St. Vincent. Birds seem never to have been common on the last-named island, a fact recorded by Ober in 1878.

On my first visit to St. Vincent on August 10, 1901, I was struck with the scarcity of birds as compared with the same or closely related species on Grenada, from which island I had come. Calospiza I did not meet with at all, although I had found *C. cucullata* common enough at Grenada. Elaenea, Pyrrhulagra, the black Coereba, Columbigallina, Holoquiscalus, and Merula could hardly be called even fairly common, although I had seen plenty the day before at St. George's. Even the little "Grass-bird" (*Tiaris bicolor omissa*) was comparatively few in numbers, although as a rule abundant on all the Lesser Antilles.

When I next saw the island, on October 19, 1903, coming from Barbados, the contrast between the conditions on St. Vincent and

those on the island I had just left was very striking; but I cannot say I noticed that the birds about Kingstown were much, if any, fewer than on my previous visit.

Unfortunately, I did not go into the woods when I was first on the island; but Lister, writing in 1880, gives the impression that Cinclocerthia, Catharopeza, Myadestes, Geotrygon, and Amazona were rather common in his time. Ober says that *Troglodytes musicus* was of very frequent occurrence in 1878. Cinchlerminia apparently has always been rare. Lister did not find it, nor did Ober obtain any specimens of it, although he heard its "unmistakable whistle" and saw "it as it flitted by in the dusk of the high woods."

At the present time *Amazona guildingii* must be put down as decidedly uncommon; and if another hurricane should occur within the next few years it is doubtful whether the species could survive it.

Catharopeza bishopi I failed to find at all. I made a special search for this bird as I was particularly anxious to obtain a good series, but could discover no trace of it anywhere. Ober says that it was found "in the crater and dark gorges of the Soufrière." If it were confined to that district there can be no doubt as to its fate. Lister records it as "confined entirely to the high woods" but does not specify at what points he met with it. As the Soufrière was the most frequently visited portion of the wooded area (there being a rest-house near the summit, accessible by a bridle path, where parties often spent the night) he might very well have seen it there only. As no one else mentions it, and the natives of the island, even the manufacturers of "mountain dew" whose occupation keeps them largely in the most remote districts, are wholly unacquainted with it, it must be considered as extremely rare, if it is still to be found at all.

Cinclocerthia ruficauda tenebrosa is now very rare, although it may possibly be found in certain remote localities. I spent many days in the high woods in localities where this bird used to be common but neither saw nor heard one.

Myadestes sibilans I did not obtain, although I searched for it at many points on the higher ridges and about the summit of Mt. St. Andrew, where it used to be of frequent occurrence. Its note is well known to many of the people on St. Vincent, but I could

find no one who had heard it since the eruptions. Probably this bird is to be found yet in certain places, as it is hard to believe a species as common as this was, has entirely disappeared.

Cinchlerminia I did not meet with, nor could I find *Geotrygon montana*. The latter bird is probably gone, as the mongoose (Herpestes), which is now abundant all through the St. Vincent woods, finds this bird an easy victim, and has very seriously reduced its numbers, if not actually extirpated it from some of the other islands (as Grenada) which have suffered neither hurricanes nor eruptions in recent years.

Locally Extinct Species.

The early writers on the ornithology of Barbados (Ligon, Hughes, Schomburgk) mention nine birds as occurring on that island which are unknown to-day as residents. They are: a grebe, probably *Podilymbus podiceps* (Hughes; Schomburgk, "*Podiceps dominicus*"), a hawk, very likely *Buteo antillarum* or a closely related form (Ligon; Schomburgk, "*Buteo borealis*"), the Purple Gallinule, *Ionornis martinica* (Hughes), the Ramier, *Columba squamosa* (Hughes, recorded as a visitor), a parrakeet, ? Conurus (Hughes; Schomburgk, "*Psittacus passerinus*"), an owl, possibly *Strix nigrescens* or a closely related form (Schomburgk, "*Strix flammea*"), a trembleur, Cinclocerthia (Ligon; Hughes; Schomburgk, "*Turdus jamaicensis*"), a "wren," Allenia (Ligon; Hughes), and a "thrush," ? Margarops (Hughes; Schomburgk, "*Turdus musteli-nus*")

In St. Vincent the Mountain Ground Dove, or "Perdrix" (*Geotrygon montana*) and the normally colored form of *Coereba atrata* (= *C. saccharina* Lawr.) seem to have disappeared. Some of the other birds which I failed to find, are possibly extinct, but further investigation is necessary to determine the question satisfactorily.

The normal form of *Coereba wellsi* appears no longer to exist on Grenada, although it is abundant on all the Grenadines.

Introduced Species.

A number of birds foreign to the fauna of the West Indies have been introduced into these islands by man, and some species have been introduced from neighboring localities.

At Barbados, *Merula gymnophthalma* has been introduced from Grenada and now breeds. *Mimus gilvus*, also from Grenada, seems to be gaining a foothold. *Sicalis arvensis luteiventris* is now very abundant in St. Phillip's and part of Christ Church parish. *Mimus polyglottos orpheus* has been recently introduced from Jamaica, but has not yet nested. I obtained a specimen of *Estrelda astrild* in a pasture in St. Joseph, and have seen *Paroaria cucullata* and *Melopsittacus undulatus* at large in Hastings. These three last were probably escaped cage birds, as I could find no evidence that they had been intentionally liberated. Many additional species have been found in an apparently feral state on Barbados, but as none of them appear to have become established, a list of them would be merely a waste of space.

In St. Vincent the English Pheasant (*Phasianus colchicus*) has been liberated on some of the Grenadine dependencies, but did not long survive. The Guinea Fowl (*Numida meleagris*), which is common in a domesticated state in all these islands, has been allowed to run wild on Balliceaux. The Venezuelan Quail (*Eupsychortyx sonninii*) has been naturalized on Mustique, and the "cocorico" (*Ortalis ruficauda*) on Bequia and Union Island. The Grenada Blackbird (*Holoquiscalus luminosus*) was brought into the leeward district of St. Vincent from the Grenadines, but seems to have disappeared. The "tickbird" (*Crotophaga ani*) is supposed to have been introduced into the island in the sixties from Tobago by a Mr. Chapman, and is said not to have existed there previously. The natives at the present time usually refer to it as the "Chapman-bird" for this reason.

Exported Species.

The Barbados Blackbird (*Holoquiscalus fortirostris*) has been introduced into St. Croix, St. Kitts, Antigua, and Demerara. So long ago as 1848 mention is made of its introduction into British Guiana. Schomburgk says that these birds are "said to have been introduced into Demerara, where they are now numerous. As a counter-present, Barbados received its crapeaux (*Bufo agua*) from that colony."

The Mongoose.

The mongoose (Herpestes) has been introduced into Barbados, St. Vincent, and Grenada. It is now thoroughly at home everywhere, is very abundant, and is found in all situations, even in the depths of the high woods on the two last-mentioned islands, although it does not occur on any of the Grenadines. Since its advent the ground doves (Columbigallina) have become much fewer on these islands, while *Geotrygon montana* appears to have entirely gone from St. Vincent, and to have become very rare on Grenada. Other birds are also affected, though to a less degree.

The West Indian Avifauna.

There are about 300 species of birds peculiar to the West Indies, of which about 200 occur in the Greater Antilles only, and 90 in the Lesser only. The remainder are species of more or less wide distribution. Of genera there are 41 confined to the West Indies. Pyrrhulagra and Margarops are of rather general distribution, while of the remainder, 28 are Greater Antillean (one of these, Mimocichla, having a representative in the Lesser Antilles on Dominica) and 11 Lesser Antillean (although two of these, Sericotes and Bellona, occur on St. Thomas, and the latter also on Porto Rico). These Lesser Antillean genera are: Eulampis, Sericotes, Bellona, Gmelinius[1] Melanospiza, Leucopeza, Catharopeza, Cinclocerthia, Rhamphocinclus, Allenia, Cinchlerminia.

In the Greater Antilles the resident species appear to have been derived mainly from Central America, with many accessions from North America, especially in the Bahamas and Cuba. The Bahamas, owing to their oceanic character, have an avifauna of comparatively recent origin, consisting largely of derivatives from North American stock, but apparently related more closely to the Greater Antilles, particularly to Cuba. The single peculiar genus, Callichelidon, is of rather uncertain status.

Jamaica appears to be the most important faunally of the Greater Antilles, and contains the largest number of peculiarly West Indian

[1] Gmelinius Boucard (type *G. bicolor*), Gen. Hummingbirds, p. 108, 1892.

species. Although Cuba has the same number of endemic forms, many of them are evidently of North American origin, and cannot therefore be considered faunally as important as those of Jamaica. Haiti has two more peculiar genera than Jamaica, but it has only 31 peculiar species as against 43 on Jamaica, and only 48 West Indian forms as against Jamaica's 60. Toward the east the avifauna diminishes in intensity, Porto Rico having but one peculiar genus, 10 West Indian genera, 18 peculiar species, and 37 West Indian species, while St. Thomas contains 4 West Indian genera, 1 characteristic species, and 11 West Indian forms.

Passing to the Lesser Antilles, we find that the group comprising Guadeloupe, Dominica, Martinique, and St. Lucia is the most important, as it contains 46 peculiar species and 5 peculiar genera. In this group should also be placed Montserrat and the northern end of St. Vincent. This gives us 6 peculiar genera and 49 peculiar species. The Lesser Antillean genera not included entirely within these limits are: Eulampis (Nevis to St. Vincent), Sericotes (St. Thomas to Grenada, and Barbados), Bellona (Porto Rico to Grenada, and Barbados), Cinclocerthia (St. Kitts to St. Vincent), Allenia (St. Eustatius to Grenada). The included genera are: Gmelinius (Dominica), Melanospiza (St. Lucia), Leucopeza (St. Lucia), Catharopeza (St. Vincent), Rhamphocinclus (Martinique and St. Lucia), Cinchlerminia (Montserrat to St. Vincent).

In this group of islands as defined the following species call for special mention. *Aestrelata ? haesitata* formerly occurred in the mountains of Guadeloupe and Dominica. *Setophaga ruticilla* is known as a resident on Dominica only. This appears to be an isolated colony from North American stock, comparable to the case of *Erismatura jamaicensis* and *Querquedula discors*, both of which breed in the Grenadines. *Nomonyx dominicus* (Guadeloupe and Dominica), *Guara alba* (Dominica), *Melanerpes lherminieri* (Guadeloupe), and *Mimocichla albiventris* (Dominica) represent colonies of Greater Antillean forms, while *Saltator guadeloupensis* (Guadeloupe, Dominica, and Martinique), *Ceryle stictipennis* (Guadeloupe and Dominica), *Antrostomus rufus* (St. Lucia), *Urubitinga anthracina cancrivora* (St. Vincent), and *Regerhinus uncinatus* (Grenada)[1] are unmistakably South American. The parrots of this region

[1] The continental species which have worked up from Trinidad and Tobago are not considered in this connection.

also (*Amazona imperialis*, *A. bouqueti*, *A. versicolor*, and *A. guildingii*) are related to *A. vinacea* of South America, while those of the Greater Antilles (except *A. agilis* and *A. vittata*) belong with *A. albifrons* of Central America.

Two of the Lesser Antillean species (and genera), *Sericotes holosericeus* and *Bellona exilis*, as mentioned above, have habitats overlapping Greater Antillean territory, while with other species the reverse is the case. These latter are *Poecilonetta bahamensis* (south to Guadeloupe), *Dendrocygna arborea* (south to Antigua), and *Phoenicopterus ruber* (Anegada, and formerly Antigua and Guadeloupe).

The islands whose avifauna forms the basis of the present paper (Barbados, St. Vincent, the Grenadines, and Grenada) are perhaps the most interesting of all the Lesser Antilles. Barbados, like the Bahamas, is oceanic, while the others show the diminishing intensity of the West Indian fauna as we go southward, correlatively with the increasing number of South American forms.

In the discussion of the avifauna of St. Vincent, the Grenadines, and Grenada, the first thing that claims our attention is the South American element. Trinidad has, according to Chapman, 199 resident land birds, all of which are continental, or closely related to continental forms. On Tobago we find 65 resident land birds, all but 6 of which occur (or have closely related forms which occur) on Trinidad; but these 6 (including *Mimus gilvus* and *Ortalis ruficauda*[1]) are all of South American stock, some of which may yet be found in Trinidad. Grenada has 13 birds common to it and Tobago, and all but one of these (*Mimus gilvus*) common to it and Trinidad, while three others (*Calospiza cucullata*, *Troglodytes grenadensis*, and *Merula nigrirostris*) are localized forms from purely South American stock.[2] On the Grenadines there are only 8 of these continental birds, *viz.*: *Merula gymnophthalma*, *Sporophila gutteralis*, *Mimus gilvus*, *Elaenea martinica flavogastra*, *Molothrus atronitens*, *Tyrannus melancholius satrapa*, *Myiarchus tyrannulus tyrannulus*, *Muscivora tyrannus*, while *Chaetura poliura*, Calospiza, *Merula nigrirostris*, and Troglodytes are lacking, although all four reappear on St. Vincent.

[1] Claimed by some to have been introduced from Venezuela, although originally described from Tobago.

[2] Troglodytes occurs northward to Guadeloupe; Calospiza and *Merula nigrirostris* are found also on St. Vincent.

The distribution of these South American forms on the Grenadines is as follows. *Merula gymnophthalma* occurs in all favorable localities throughout the islands. *Mimus gilvus* is everywhere very abundant. *Myiarchus tyrannulus tyrannulus* is common everywhere. *Elaenea martinica flavogastra* I obtained only on Bequia and Mustique, but it very likely occurs on the other islands. *Molothrus atronitens* is common as far north as Canouan. It is, however, of recent occurrence. *Tyrannus melancholius satrapa* I obtained on Union Island. *Sporophila gutteralis* is locally common at Carriacou, where, however, it is a recent arrival. *Muscivora tyrannus* is common on Carriacou in the wet season

On St. Vincent these South American forms are reduced to four of those found on the Grenadines, with four more which do not occur on the smaller islands. They are: *Elaenea martinica flavogastra*, *Mimus gilvus*, *Merula gymnophthalma*, *Myiarchus tyrannulus tyrannulus*; and *Merula nigrirostris*, Troglodytes, Calospiza, *Chaetura poliura*. In addition to these we have as a resident *Urubitinga anthracina cancrivora*, corresponding with *Regerhinus uncinatus* of Grenada.

Besides these established species I obtained a specimen of *Florisuga mellivora* on Carriacou, met with a stray example of *Sporophila gutteralis* at Kingstown, St. Vincent, and found a single *Anthracothorax gramineus* on Union Island, all of which were apparently accidental visitors, although it is not at all improbable that they may become residents at some future time.

Turning now to characteristically West Indian genera, we find that Grenada has only four, *viz.*: Pyrrhulagra, Allenia, Bellona, Sericotes; and the Grenadines only the two hummingbirds, although Allenia was for a time resident there. The first of these four genera is of rather wide distribution throughout the West Indies, the species in question (*P. noctis*) having roughly the same range as the representatives of the other three genera.

St. Vincent has these four genera, and in addition four others peculiar to the Lesser Antilles; they are: Eulampis, Cinchlerminia, Cinclocerthia, Cartharopeza, the last being confined to that island.

Besides these characteristic genera, St. Vincent has the following forms which are worthy of note: Myadestes, *Elaenea martinica martinica*, Cypseloides, *Chaetura acuta*, *Bellona exilis* (*ornata*), Amazona.

The first three, while not primarily West Indian, are more or less characteristic of that region, and their absence from Grenada is noteworthy. *Chaetura acuta* is Lesser Antillean (Guadeloupe to St. Vincent). The crested hummingbird of St. Vincent is *Bellona exilis* (Porto Rico to St. Vincent) *ornata* (St. Vincent) instead of *B. cristatus* of Grenada, the Grenadines, and Barbados. *Amazona guildingii* of St. Vincent also connects that island with those to the north, being closer to *A. imperialis* of Dominica than to any other species. There is no good evidence that any parrot ever existed on Grenada.

The avifauna of St. Vincent shows a correlation with that of Grenada; in each island Calospiza occurs, the two species (*C. versicolor* and *C. cucullata*), although perfectly distinct, being closely related; both islands have dimorphic species of Coereba that occur in the normal coloration of the genus, and also entirely black (*C. atrata* and *C. wellsi*); and both have closely related subspecies of *Pyrrhulagra noctis*.

Now those forms common to St. Vincent and the islands toward the north, but not occurring on Grenada, *viz.*, Eulampis, Cinchlerminia, Cinclocerthia, Myadestes, Cypseloides, Amazona, *Chaetura acuta*, *Elaenea martinica martinica*, and *Bellona exilis* are, with the exception of the two last, inhabitants of the high woods, these two only occurring both there and in the lowlands. Moreover, *Elaenea martinica martinica* is only found in the northern and middle parts of the island, and is absent from the region about Kingstown.

The forms common to St. Vincent and Grenada (*viz.*, *Elaenea martinica flavogastra*, *Mimus gilvus*, *Merula gymnophthalma*, *Pyrrhulagra noctis*, *Sericotes holosericeus*, and *Myiarchus tyrannulus tyrannulus*) are primarily lowland species, and *Elaenea martinica flavogastra*, *Merula gymnophthalma*, and *Mimus gilvus* are, the two first entirely, and the last largely, restricted to the Kingstown valley. *Merula nigrirostris*, the black form of *Coereba atrata*, Calospiza, and *Allenia albiventris* occur very generally on the island, but all are rare in the high woods. *Troglodytes musicus* (which is nearer *T. mesoleucus* of St. Lucia than to *T. grenadensis*) occurs everywhere.

Thus we find that faunally St. Vincent is divisible into two regions, the higher altitudes, and particularly the vicinity of the

Soufrière in the northern part of the island, being a continuation of the Montserrat-St. Lucia district, while the lowlands, especially the Kingstown valley in the southern part of the island, belong faunally to Grenada and the Grenadines.[1]

Certain other species not mentioned above are worthy of passing notice. *Progne dominicensis* and *Tiaris bicolor omissa*, as would be expected, occur in all favorable localities; *Vireo calidris barbadense*, *Euphonia flavifrons viscivora*, and *Tyrannus dominicensis rostratus* (the second the southern form of a Lesser Antillean species, and the others chiefly Lesser Antillean forms of West Indian species) occur in these islands, the second on St. Vincent and Grenada only, the others everywhere. The Lesser Antillean "Kili Hawk" (*Falco sparverius caribbearum*) does not occur between St. Lucia and Grenada, although found on both these islands. The mangrove cuckoos of Grenada and the Grenadines appear to be true *Coccyzus minor minor*; but a deeper-colored, large-billed form (*C. m. vincentis*) occurs on St. Vincent (and St. Lucia also). *Buteo antillarum*, a rather wide ranging species, is found on St. Vincent, Bequia (Grenadines), and Grenada, and the Lesser Antillean Owl (*Strix nigrescens*) otherwise known only from Dominica, also occurs on these three islands. A yellow warbler (*Dendroica ruficapilla*) occurs on Grenada, Carriacou, Union Island, and Prune (Grenadines), which is also known from Cozumel Island (Yucatan), St. Andrew's Island, Curaçao, Dominica, and Guadeloupe.

Two species are resident in the Grenadines which are not found elsewhere in the Lesser Antilles: the Ruddy Duck (*Erismatura jamaicensis*) and the Blue-winged Teal (*Querquedula discors*). The Whistling Duck (*Dendrocygna discolor*), not otherwise known from the Lesser Antilles: is casual as far as St. Vincent, and possibly breeds on Barbados.

The sea birds of these islands offer no peculiarities in their distribution.

The most noticeable features in connection with the avifauna of Barbados are the small number of resident land birds, and the almost entire absence of sea birds, of which but one species (*Puffi-*

[1] *Holoquiscalus dispar*, confined to this region, forms an exception as it takes the place of *H. luminosus* of the Grenadines and Grenada.

nus lherminieri) now breeds on the island, and such common forms as *Larus atricilla* and certain of the terns (Sterna, Anous) occur only as uncommon visitors. The geological structure of the island, together with its isolated geographical position, the paucity of swamps and marshes, and the almost complete destruction of the original forests, which have everywhere given place to the canefield, account satisfactorily as Col. Feilden remarks for the lack of birds.

There are at present on the island 16 resident species and subspecies, *viz.*: *Dendroica capitalis*, *Coereba barbadensis*, *Vireosylva calidris barbadense*, *Pyrrhulagra barbadensis*, *Tiaris bicolor omissa*, *Holoquiscalus fortirostris*, *Elaenea martinica barbadensis*, *Tyrannus dominicensis rostratus*, *Sericotes holosericeus*, *Bellona cristata emigrans*, *Zenaida zenaida aurita*, *Columbigallina passerina trochila*, *Butorides virescens maculata*, *Gallinula galeata*, *Fulica caribaea*, *Puffinus lherminieri*.

It will be noticed at once that most of these species and subspecies, and all of these genera are of very general occurrence throughout the Lesser Antilles. Six species and subspecies, *viz.*: *Dendroica capitalis*, *Holoquiscalus fortirostris*, *Coereba barbadensis*, *Elaenea martinica barbadensis*, *Pyrrhulagra barbadensis*, *Bellona cristata emigrans*, are recognizable forms, peculiar to Barbados.

Evidently, then, the avifauna of Barbados, as might be expected in an oceanic island so situated, is wholly made up of very generally distributed types, birds which, from their abundance in this region, would be theoretically the first to reach any new land in the vicinity.

Barbados being generally flat, with very little physiographical differentiation, and with almost the whole island under the same conditions of cultivation, its birds are generally distributed, and not grouped into faunal zones as are those on other islands, although, of course, certain species are rather more partial to pastures (as Columbigallina), and others to woodlands (as Elaenea and Tyrannus). Vireosylva alone among the land birds has a restricted habitat, being confined to certain portions of the Scotland district. The one sea bird (*Puffinus lherminieri*) is only found on a small rock off the shores of St. Lucy's parish.

In former times, if we may place any reliance on the writings of Hughes (1750), Ligon (1763), and Schomburgk (1848), there were also resident on Barbados the following: Allenia, Cinclocerthia, ? Margarops, ? Conurus, *Buteo* (*? antillarum*), *Strix* (*? nigrescens*),

?Podilymbus podiceps, *Ionornis martinica*; while according to Hughes the Scaled Dove (*Columba squamosa*) used to visit the island regularly. It is probable that most, if not all, of these birds did occur when Barbados was clothed in natural forest, as Allenia is a common and widely distributed form; Cinclocerthia is common from Nevis and Barbuda to St. Lucia, and used to be on St. Vincent; Margarops occurs from the Bahamas to St. Lucia, and has been obtained in recent years on Barbados; *Buteo antillarum* is abundant on the neighboring islands; *Strix nigrescens* is common on Dominica, St. Vincent, and Grenada; *Podilymbus podiceps* occurs throughout the West Indies, and has been found on Barbados; and Ionornis is a common bird in the West Indies wherever there are swamps. No parrakeet is at present known from the Lesser Antilles; but Hughes and Schomburgk both mention one, and there appears to be good evidence that these birds formerly existed on Martinique and Guadeloupe, so I believe we are safe in admitting it, at least provisionally.

Owing to the rather general and intelligent interest taken in ornithology at Barbados, and to the fact that all parts of the island are accessible to the sportsman, and also because of its geographical position away from the other islands and not protected, so to speak, at all by them, a rather full list of migrants and accidental visitors has been recorded, no less than 50 from North America (including the shore birds), 13 from neighboring islands and the adjacent mainland, and 5 from the Old World.

Annotated List.

Podilymbus podiceps (Linn.). Pied-billed Grebe.— The Pied-billed Grebe is a rather uncommon resident on Grenada, Isle Ronde, and Carriacou. There is a specimen in the British museum from Barbados.

Mr. J. H. Riley (:04b, p. 278) finds that two birds of this species from Antigua and Barbuda differ slightly from North American examples. Mr. B. S. Bowdish remarks (Auk, vol. 19, p. 357, 1902) that a specimen obtained by him at Aguadilla, Porto Rico, is

smaller than northern birds; an examination of a series from the West Indies may demonstrate a recognizable local race.

Hughes (**1750**, p. 71) mentions a grebe "of the bigness and much the color of the American quail" as resident in Barbados in his day, and refers to it under the name of "The Two-Peny Chick." Sir Robert Schomburgk includes *Podiceps dominicus* in his list of the birds of Barbados, calling it the "Two-penny Chick," a name at present used on the island for *Porzana carolina*. Col. Feilden ('**89a**, p. 503) refers the grebe mentioned by these two authors to *Podiceps dominicus*, following Schomburgk; but as that species is unknown from the Lesser Antilles, whereas *P. podiceps* is of very general occurrence and has been recently taken on Barbados, I have thought it best to refer it to the latter.

NOTE.— *Colymbus holboelli*, recorded by various authors (following Wells, '**86**, '**86a**, *Podiceps holboelli*) from Grenada (Isle Ronde. Grenadines) is in reality *Erismatura jamaicensis* (*q. v.*) wrongly identified.

Oceanites oceanicus (Kuhl). WILSON'S PETREL.—Recorded from Grenada and Carriacou. Without doubt of casual occurrence near all these islands.

Puffinus lherminieri Less. DIABLOTIN; AUDUBON'S SHEARWATER.— This is the only sea bird resident on Barbados. It breeds regularly, though in small numbers, on Bird Rock, off the northern coast of St. Lucy's parish, from which place Col. Feilden ('**89**, p. 60) has obtained the eggs in March.

Hughes says, speaking of Barbados in 1750: "The several cavities in the cliff facing the sea [in St. Lucy's] are proper dens for Raccoons, and such wild beasts. They are likewise a place of safety for several sea-birds to breed in, especially at a place called 'Bird Rock,' where are to be seen at most times of the year a great many of their nests and eggs. The young ones are sharp-billed, wet-footed, and very fat, but taste fishy. The old ones are seldom or never seen in the day time, for they are obliged to range to so great a distance from the shore for food that they have been seen scores of miles from land."

I have seen Audubon's Shearwater in Kingstown Bay, St. Vincent, and it is sometimes common about the entrance to Bequia Harbor. It occurs throughout the Grenadines, breeding, according to Wells, on most of the small islets about Carriacou, especially on Bonaparte Rocks.

About Grenada it is not rare, and breeds commonly on "Mouchoir Quarré" and the Labaye Rocks. Wells says that formerly numbers of the dried young of this species used to be brought into the market at Grenville (Labaye), obtained on the former islet. He says of some he caught on Labaye Rocks: "The birds on being brought out into the light appeared to be quite foolish, and, beyond a feeble attempt to bite, seemed to make no effort to escape. I kept them alive for some days; they would take no food during the day, remaining perfectly quiet; but at night they fed on scraps of fish, and at intervals uttered a peculiar cry like a cat-howl."

This little bird when flying skims along close to the surface of the water, acting in every way much like its larger northern relatives.

The single egg is dull white in color.

Phaethon americanus Grant. Yellow-billed Tropic-bird. — There is a skin of this bird in the British museum which was procured on St. Vincent in 1890, by Mr. G. Whitfield Smith, F. L. S., the present commissioner of the island of Carriacou. There are no other records.

Phaethon aethereus Linn. Paille-en-queue; Bo's'n; Red-billed Tropic-bird. — This bird is occasionally seen at Barbados. One was captured near Chancery Lane after a gale in 1877 but was not preserved.

In February, March, and April it is common along the leeward coast of St. Vincent, where it breeds in holes in the cliffs. There is a considerable colony of them near Old Woman's Point, just west of Kingstown, and another at Layou.

At Bequia they breed in numbers in the inaccessible cliffs of Bequia Head, but I did not find them elsewhere. Usually they are not very common among the Grenadines, but great numbers breed on Battowia and Balliceaux, and there are other colonies on Frigate Island, Rose Rock, Kick-'em-Jenny, and Les Tantes, between Carriacou and Grenada. It is locally common about the cliffs of the last-named island.

The wing beats of this and the preceding species are continuous and rather rapid, somewhat suggesting the flight of certain ducks. When near the cliffs, however, they often sail about, after the fashion of Noddies (Anous). Both the Yellow-billed and the Red-billed Tropic-birds are often met with very far from land.

The egg of the Red-billed Tropic-bird is deposited in a hole in a cliff or under some projecting ledge or rock, and is light purplish in color, minutely sprinkled with neutral tint and claret brown.

Sula cyanops (Sundev.). Blue-faced Booby. — Occurs sparingly on Kick-'em-Jenny, and probably also at Battowia. The eggs are uniform dull white.

Sula leucogastra (Bodd.). Booby; Fou. — Abundant, except in the vicinity of Barbados. This bird is always to be found along the leeward coast of St. Vincent, where some of them may usually be seen toward evening perched on the cliffs, where they spend the night. The majority, however, begin to fly down the coast at about three in the afternoon, making for Battowia, which island is the favorite roosting place of all the sea birds in this region.

These birds are usually seen in little companies of three to eight, often containing one or more individuals of other species, most commonly *S. piscator*. Hundreds of boobies, mainly of this species, nest at Battowia and Kick-'em-Jenny, and there is said to be a large colony on Little Tobago (off Petit Martinique).

The eggs are one or two in number, dull greenish blue, and are laid in a coarse nest, placed usually in low trees (often several on one tree) or on the ground. The breeding season is from February to May.

Sula piscator (Linn.). White Booby; Fou Blanc; White-tailed Booby. — The White Booby is often seen flying about the channel between St. Vincent and Bequia, and occasionally about the leeward coast of St. Vincent, in company with others of the genus. It is said to breed commonly on Battowia, toward which island it may be seen making its way every evening to roost. It nests in numbers on Kick-'em-Jenny, and is sometimes seen about the islands in that vicinity, and along the coasts of Grenada.

The plumage in which the bird is brown, with the exception of the tail and upper and under tail coverts, which are white, is more common here than the white form, and individuals of this color are often seen in little companies by themselves, or with white adults, or with Common Boobies (*Sula leucogastra*).

The nest, like that of *S. leucogastra* is a loose structure, usually placed on low trees or bushes; eggs one or two, dull greenish.

NOTE.— Wells ('**86a**, p. 630) says that there is "a small duck, quite black, occasionally found in the sea [about Grenada]. I shot one a couple of years ago." The only black duck-like bird which is maritime in habit and which might stray into these waters is the Brazilian Cormorant (*Phalacrocorax brasiliensis*), which possibly may range as far north (in the West Indies) as Grenada, as it occurs about Trinidad, and either this or a closely allied form is abundant along the Venezuelan coast. Mr. Wells was very little acquainted with birds, except with those of Grenada (*cf.* his identification of *Erismatura jamaicensis* as *Colymbus holboelli*), and as this little cormorant more or less resembles some ducks in general habits, he might very well have referred to it as a duck.

Pelecanus occidentalis (Linn.). BROWN PELICAN; GRAND-GORGE.— The Brown Pelican is an irregular visitor to Barbados. In 1886 and 1887, according to Col. Feilden, it appeared in flocks of hundreds.

This bird occurs along the shores of St. Vincent, mainly about Young's Island and Calliaqua, but is not at all abundant as a rule.

It is common throughout the Grenadines, especially about Carriacou, on the Pillories (near Mustique), about the leeward coast of Mayreau, and in the vicinity of Bloody Bay and Clifton, Union Island. It occurs mainly in the winter months, and almost wholly disappears in the spring, but returns in early summer. The Brown Pelican does not breed anywhere in these islands, but is merely an annual visitor, possibly from southern North America and the Greater Antilles. Ober says that this bird "breeds on the rocks north of Grenada, as well as through the Grenadines"; but as after careful search and exhaustive inquiry I could find not the slightest sign of their ever having done so, I cannot attach any weight to the statement. Ober, himself, never visited the localities mentioned and probably relied on the assertions of natives at St. Vincent or at Grenada, who are (the lower classes) absolutely unreliable. He also gives the Spoon-bill (*Ajaia ajaia*) as casual in Grenada, and the Long-billed Curlew (*Numenius longirostris*) as having occurred on St. Vincent (there are no Lesser Antillean records) apparently on the same authority.

Dutertre says that in the year 1656 there was a great mortality among birds of this species, and that the shores of St. Lucia, St. Vincent, Bequia, and the Grenadines were strewn with their dead bodies. The Brown Pelican occurs all about the coasts of Grenada.

NOTE.— I have been told by several trustworthy persons that White Pelicans have occasionally been seen among the Grenadines. Although there is a possibility that they may have been examples of *P. erythorhynchos* (which Mr. J. H. Fleming tells me he has seen in the harbor of St. John, Antigua), still they might have been Brown Pelicans somewhat lighter on the back than usual.

Fregata aquila (Linn.). COBBLER; FRIGATE BIRD; MAN-O'-WAR.— The Frigate Bird, or, as it is called locally, the Cobbler, is rare at Barbados; but Col. Feilden writes that he has observed it passing over the island at a great height, and it is occasionally shot there. Sloane (**1707**, p. 30) says that he first observed them on nearing Barbados. Both he and Ligon (**1673**, p. 61; **1674**, p. 103) write that the appearance of this bird is popularly supposed to foretell the coming of a ship. He also noticed that "there are more of these in the firm land of America than in these isles," and that "it follows the Pelican in the air to catch its dung for food."

About St. Vincent, the Grenadines, and Grenada this bird is rather common, but not so abundant as along the Venezuelan coast, particularly in the vicinity of Margarita Island. In the Grenadines they breed in numbers on Battowia, whence the young are sometimes taken for food.

The nest is a loosely built structure, placed either on the ground or in low trees. The eggs are one or two, dull greenish white.

Ardea herodias Linn. GREAT BLUE HERON; GRAY GAULDING; CRABIER MONTAIGNE.— A regular and not uncommon visitor to these islands, arriving in October. Col. Feilden says that it arrives at Barbados in October and November in parties that sometimes consist of ten or twelve individuals. Hughes, writing in 1750, speaks of this bird as a winter visitor to Barbados, saying that it is very seldom seen there, but is much commoner at Antigua.

This heron is found every winter along the leeward coast of St. Vincent, especially in the vicinity of Young's Island and Calliaqua.

On Carriacou, Wells writes that on one occasion he saw eight of them together in Harvey Vale pasture.

Wells records it from Grenada as "a migrant; not numerous."

Herodias egretta (Gmel.). AMERICAN EGRET.— Col. Feilden says: "I procured one at Graeme Hall swamp (Barbados) on July 4, 1888, an adult female in beautiful plumage. It was alone at the time." There are no other records for these islands.

Egretta candidissima (Gmel.). SNOWY HERON.— This bird

is of casual occurrence on St. Vincent, the Grenadines, and Grenada. In October, 1903, one of them could be seen almost every day about the mouth of the Richmond River, St. Vincent.

Wells gives it as uncommon on Carriacou, but he never found it on Grenada, although Ober took a specimen there.

Ober in his account of this bird in Grenada must have had in mind the immature of *Florida caerulea* (*caerulescens*). The Snowy Heron by no means occurs in "abundance," nor is it second to *Butorides virescens* (*maculata*) in point of numbers.

Florida caerulea caerulescens (Lath.). Blue Gaulding; White Gaulding; Little Blue Heron.— St. Vincent, owing to the absence of swamps, offers but few attractions to birds of this class. The Blue Gaulding is, however, occasionally seen along the shores, especially about the bases of the cliffs on the leeward coast, in the vicinity of Young's Island, near Calliaqua, and about the mouth of the Richmond River, on the now barren ground.

On the Grenadines this bird is common, being, in fact, the most abundant of all the herons. It is particularly numerous in the swamps at Harvey Vale, Carriacou.

On Grenada this heron is found everywhere on the seacoast and in all the swamps. It is mainly a maritime species in these islands, and subsists largely upon fish, which it is very expert in catching. It is generally seen feeding out on a coral reef, or in the shallow water near shore. After heavy rains, however, it frequents the low-lying pastures, and is very common about the Beausejour and Harvey Vale Flats, Carriacou.

Its flight is particularly strong, and it is often seen high in air passing from one small island to another.

I was unable to find any nests of this species in the swamps on Carriacou, as it usually breeds on the small islets off the coast.

The nest is loosely constructed of dry sticks, and often several are placed on the same tree. The eggs are two, sometimes three, rarely four in number, and are bluish green.

Butorides virescens maculata (Bodd.). Gaulding; Little Crabier; Hyallee; Green Bittern.— I have referred the Green Bitterns of these islands (as has Mr. Riley, :04b), to Boddaert's *Cancroma maculata* (Boddaert, Table pl. enl., p. 54, 1783, Le Crabier tachété de la Martinique, Pl. enl., 912) as West Indian specimens agree in being smaller than those from North America,

although there appears to be no difference whatever in color in perfectly fresh examples. The differences in size are apparent from the following table. The measurements are in millimeters.

Butorides virescens maculata.

Sex.	Locality.	Wing.	Tail.	Tarsus.	Culmen.
♂	Barbados	157	63	43	57
♂	"	163	62	49	58
♂	"	162	54	47	53
♂	"	165	59	46	57
♂	" juv.	163	65	46	52
♀	"	160	46	47	55
♀	"	177	62	48	57
♀	"	160	65	46	60
♀	" juv.	142	48	46	46
?	Bequia	164	68	50	60
♂	"	169	68	48	59
♂	Carriacou	160	60	46	57
♂	Grenada	171	64	49	56

Butorides virescens virescens.

♂	Wayland, Mass.	181	70	51	63
♀	" "	167	68	48	62
♀	" " juv.	176	66	50	56
♂	St. Mary's, Ga.	168	66	50	50
♀	" "	186	71	48	58
♀	" "	181	76	51	61
♂	Florida	173	63	51	60
♂	"	180	73	48	63
		180	61	51	64

On Barbados this bird is fairly common in places where it is not disturbed. Col. Feilden says he has started as many as a dozen from a single tree in Valentia swamp at one time. It breeds in the grounds of Codrington college, about Joe's River, St. Joseph, and in parts of St. Andrew's. At other points it is not abundant, and, owing to constant persecution, has become very shy.

On St. Vincent the Green Gaulding is not very numerous, and is found mainly along the lower reaches of the rivers, sometimes along the seacoast.

It occurs on all the Grenadines, being most common on Carriacou, at Harvey Vale, and is the most abundant heron on Grenada.

It nests in May, June, and July, the nest and eggs being exactly like those of this species in the north.

Nycticorax nycticorax (Linn.). Black-crowned Night Heron.— On June 8, 1904, while in Grenada, I examined a fine adult skin of this bird (unsexed) which had been obtained about a month previously by Mr. Charles Vernet near St. George's.

At Harvey Vale, Carriacou, on August 29, 1904, I saw a fine adult of this species in the swamp near the oyster beds, but failed to obtain it.

The British museum possesses skins of this heron that were obtained on St. Vincent by Mr. G. Whitfield Smith, and two which he procured on Grenada, in 1890.

Other West Indian records are: Jamaica, Bahamas, Cuba, Isle of Pines, Porto Rico, St. Kitts, Antigua, and Trinidad.

This bird is probably a rare resident in the swamps throughout the Lesser Antilles.

Nyctanassa violacea (Linn.). Crabier; Yellow-crowned Night Heron.— On September 12, 1903, at Barbados, I purchased an immature female of this species from a negro near Bathsheba, St. Joseph, who had caught it a few days previously. It was one of a flock of seven which had appeared in the vicinity of Bathsheba. This particular bird had managed to get inside of a kitchen house in a small village, and was there captured.

The Yellow-crowned Night Heron is uncommon on St. Vincent. On October 27, 1903, while hunting for bats in a large cave near the town of Barrouallie, I surprised one of these birds that had evidently gone in there to spend the day. The British museum has several skins from this island, obtained by Mr. G. Whitfield Smith. It is unknown to most of the inhabitants, but appears to occur regularly about Calliaqua and Young's Island.

On Bequia it is not uncommon, although from its habit of spending the day among the mangrove roots it is rarely seen unless a careful search is made for it. I met with it on Mustique, Mayreau, Canouan, and Prune. On Union Island it is very common in the vicinity of a large mangrove-bordered pond near the northern coast, and is often seen at other points. On Carriacou it is abundant, especially about Harvey Vale where one or two may be seen in the pastures at any time hunting for crabs. It is common on Grenada, especially near the sea.

This bird is mainly nocturnal, coming out of the mangrove swamps at dusk to hunt for crabs in the pastures and to fish along

the coast. Stray individuals are, however, often seen during the day. In general habits it much resembles *Nycticorax nycticorax* and its cry is similar. It is very good eating, and is often shot for food. The Yellow-crowned Night Heron may be considered as abundant in these islands wherever there are swamps.

The rudely constructed nests are built in the mangrove trees in the swamps; the eggs are usually three, blue green in color.

Anas boschas Linn. MALLARD. — Hughes (**1750**, p. 77) says: "The very few [wild ducks] that migrate to this island are of the same make and species with those in England." Had he had in mind any other duck than the Mallard it seems probable that he would have spoken more at length.

At the present time this duck is a rare migrant, occurring on St. Vincent, the Grenadines (Mustique and Carriacou), and Grenada.

Querquedula discors (Linn.). BLUE-WINGED TEAL.— This little duck is a common winter visitor to Barbados, St. Vincent, the Grenadines, and Grenada, occurring in flocks of from ten to twenty.

It breeds regularly at Isle Ronde in the Grenadines, where Wells obtained incubated eggs on January 3, 1883, and probably also in the swamps of Carriacou, where it is found throughout the year.

The nest is of grasses, on the ground in the swamps; the eggs are six to ten, brownish buff.

Nettion carolinense (Gmel.). GREEN-WINGED TEAL.— The Green-winged Teal is a common visitor to the ponds and swamps of St. Vincent, the Grenadines, and Grenada, arriving in October and leaving in April. Schomburgk ('**48**, p. 682) gives it as occurring at Barbados.

Hughes (**1750**, p. 77) says, speaking of "The Teal": "As this differs little, or not at all from those in England [*Nettion crecca*], it will not be necessary to give a particular description of it. It will be sufficient to observe that in England they are seen every winter, tho' hither [Barbados] they come but once a year, and very few in numbers, and some seasons none at all."

Ligon (**1673**, p. 61) mentions the teal, and gives an amusing description of how, when one is shot, the others keep coming back until all are killed.

Spatula clypeata (Linn.). SHOVELER; SPOONBILL. — Col. Feilden says that this duck is an annual visitor in small numbers during the months of October and November. There are no

records for the other islands (St. Vincent, the Grenadines, and Grenada), but probably the Shoveler is at least an occasional visitor to all of them. Cory gives it as recorded only from Jamaica, Cuba, Porto Rico, and St. Thomas.

Erismatura jamaicensis (Gmel.). Red Diver; Ruddy Duck. — The Ruddy Duck is a rare straggler to Barbados; one was obtained on September 13, 1888, and another in the fall of 1887, at Chancery Lane.

This bird is occasionally found on St. Vincent and Grenada, is a resident on some of the Grenadines, and a visitor to the others. Wells found it breeding at Lauriston swamp in Carriacou, and it is abundant at the pond at Isle Ronde, nesting in the latter part of the winter.

Wells records *Colymbus holboelli* from Grenada (Isle Ronde), calling it the "Red-backed Diver," and says: "Abundant at Isle de Rhonde Pond." The bird is, however, this species which is here locally known as the "Red Diver."

The following references, therefore, should be placed under the synonymy of this duck: —

Podiceps holboelli Wells, List birds Grenada, p. 12 (1886); Wells and Lawr., Proc. U. S. nat. mus., vol. 9, p. 633 (1886); Cory, Auk, vol. 5, p. 156 (1888); Cory, Birds W. I., p. 284 (1889).

Colymbus holboelli Cory, Auk, vol. 5, p. 156 (1888); Cory, Birds W. I., p. 284 (1889); Cory, Cat. W. I. birds, pp. 81, 185 (1892).

The nest is placed on the ground in swamps; the eggs are six to ten in number, creamy white.

Dendrocygna discolor Scl. and Salv. Tree Duck; Whistling Duck. — On September 7, 1903, when in the woods about the upper reaches of Joe's River, Barbados, I saw three of these ducks. They flew by me several times, and finally alighted in a tree some distance off, but could not be approached near enough for a shot. My little black boy immediately recognized them as "Coot." A week later I shot one of these birds from the top of an immense silk-cotton tree in this vicinity, but was unable to find it. Col. Feilden writes that in September, 1887, a flock of twenty-seven of these ducks appeared in Graeme Hall swamp, and that a wounded one was captured and taken to Dr. C. J. Manning, in whose aviary he saw it a year later, alive and well.

On February 6, 1904, while I was at Kingstown, St. Vincent, Mr. T. M. Macdonald of Wallilibou sent me a wounded bird of this species which had been caught on his estate near Barrouallie. He told me that a few days before a flock of about two dozen of them had appeared in Barrouallie Bay, and subsequently flew over to the Wallilibou estate. They were so tame that ten or more were killed by the negroes with sticks and stones. He tells me he never before met with this bird on St. Vincent.

Mr. Charles Wallace afterwards told me that a few days previous to this he had seen a flock (probably the same one) on the pond near his house on Mustique, and that he had never before observed this species.

Branta bernicla (Linn.). BRANT.— Col. Feilden says that he considers himself justified in including this goose as having certainly visited Barbados on one occasion. "My authority is Mr. J. P. Massiah, M. P., who shot the bird in question at Chancery Lane on November 15th, 1876. His accurate description leaves no doubt in my mind that the bird was of this species. During an experience of over thirty years, Mr. Massiah has never seen but this one wild goose in Barbados, nor could I hear from any other source of wild geese having been seen or obtained, except in this single instance."

This is especially interesting in being the only recorded instance of the occurrence of the Brant in the West Indies. The White-fronted Goose (*Anser albifrons gambeli*) has been taken in Cuba, the Snow Goose (*Chen hyperborea*) in the Bahamas, Cuba, Jamaica, and Porto Rico, the Blue Goose (*Chen caerulescens*) in the Bahamas and Cuba, and the Canada Goose (*Branta canadensis*) in Jamaica.

[*Vide* Doubtful Species; *Branta canadensis.*]

Catharista urubu (Vieill.). CORBEAU; BLACK VULTURE.— Mr. Francis Coull tells me that about twenty years ago two of these birds lived for a while on the Montrose estate, Grenada, but subsequently disappeared. I have been credibly informed by a number of people that this bird is occasionally seen in Grenada.

Wells records *Urubitinga anthracina* from Grenada, but it is much more likely that it was this species, as he gives it as doubtful, and usually in the case of the Urubitinga there is no possibility of a doubt, as the glaring white bands on the tail at once make it clear what the bird is. When soaring, the two birds are strikingly alike;

but it is very seldom that the Black Hawk is seen about the tree-tops.

Falco peregrinus anatum (Bonap.). Duck Hawk.— Col. Feilden obtained a female of this species from Mr. E. N. Armstrong of the Crane hotel, St. Philip's, Barbados, which was shot on the windward side of the island, November 17, 1888.

On St. Vincent a few of these hawks are seen every winter, when they attract attention by their great quickness of wing, and are distinguished by the natives from the Fish Hawk, and the local "Chicken Hawk" (*Buteo antillarum*). They are found about the cliffs of the leeward coast chiefly.

The Duck Hawk is of casual occurrence in the Grenadines. I had a bird described to me which was shot on Mustique and was probably of this species. It has not been found on Grenada.

Falco columbarius. Pigeon Hawk.— Schomburgk gives this species as resident in Barbados in his time. Although he is not confirmed by Hughes, there is a possibility that it may have bred in Barbados, as it is said to occur throughout the year on Dominica at the present time. The Pigeon Hawk is now of casual occurrence on Barbados in the winter months.

On St. Vincent it is a rather uncommon migrant; I saw one near Calliaqua in January, 1904.

Wells records this bird as a migrant, arriving in Grenada and Carriacou with the shore birds. It is probably a casual visitor to the other Grenadines.

Falco sparverius caribbaearum (Gmel.). Kili Hawk; Sparrow Hawk.— Col. Feilden says that on October 27, 1888, while driving in Christ Church parish, Barbados, a small hawk dashed past the horse's head; it was, he thinks, undoubtedly of this species.

I saw a Sparrow Hawk at Kingstown, St. Vincent, on February 6, 1904, and another at Industry estate, Bequia, December 2, 1903, but it is probable both were stragglers, as I did not see nor hear of any others in these islands, except that I was told that Mr. H. G. Selwyn Branch once took a specimen at Bequia.

On Grenada it is a rather rare resident, mainly in the windward district. I only met with it once, on the outskirts of St. George's, in May, 1904.

Buteo antillarum Clark.

ANTILLEAN CHICKEN HAWK; GREE GREE.

Buteo antillarum Clark, Proc. biol. soc. Washington, vol. 18, p. 62, Feb. 21, 1905.

Type locality.— Chateaubelair, St. Vincent.

Color.— Above brown, the feathers white at the base and margined with rufous to the tips, the white bases showing through on the nape, and giving that region a mottled appearance. Wing coverts margined all around with rufous. Lores whitish; head all around brown, the feathers margined with rufous, being darkest at base of bill and under eyes. Throat light buff, streaked with blackish brown. Breast rufous brown, mottled with light buff, more heavily toward abdomen, which is mainly light buff barred with rufous brown. Under tail coverts light buff. Thighs buff, barred with many transverse lines of rufous. Under wing coverts buff like the thighs, many of the feathers having small black central streaks. Upper tail coverts tipped with white. Tail brown, tipped with light grayish brown, with white at the extremity, crossed by two bands and an indicated third band of light grayish brown, becoming white on the inner webs of the feathers.

Iris yellowish white[1]; cere yellow; feet orange yellow; bill dark slaty.

This species differs from *B. platypterus*, to which it is most closely allied, in being smaller and much more rufous; the rufous edgings to the feathers above wider, the underparts more rufous, and the thighs buff, more thickly barred than in that bird. In the young the ground color below is buffy white, becoming darker on the abdomen and thighs. The iris is yellowish white in all stages.

A comparison of the specimens from St. Vincent with eight others from Dominica, shows that the Dominica bird is darker and more sooty above, more heavily marked on the breast, and deeper

[1] The iris of *B. platypterus* is brown; but Dr. Glover M. Allen tells me that he once obtained an immature bird of that species at Intervale, New Hampshire, which had yellow irides.

buff on the underparts, suggesting the presence of a recognizable local race on that island. The iris of the Dominica birds is given as white.

I have examined an example from Cuba (in the collection of Messrs. E. A. and O. Bangs) which agrees very well with the St. Vincent birds, except in size. It is marked "male" but is the size of the females from St. Vincent. There is a possibility that the bird is wrongly sexed.

Schomburgk gives *Buteo borealis* as a resident on Barbados. Although there is a possibility that *B. borealis* occurred on Barbados at that time (as it does at the present day on St. Kitts and in the Greater Antilles) it appears to be more probable that this species (or a closely allied form) was the one referred to, as it is common on the neighboring islands of Dominica, St. Lucia, St. Vincent, and Grenada, while *B. borealis* has never been met with so far south. Hughes does not mention any hawk; but Ligon says (**1673**, p. 60; **1674**, p. 101): "The birds of this place [Barbados] (setting two aside) are hardly worth the pains of describing, yet, in order, as I did the beasts, I will set them down. The biggest is a direct Bussard, but somewhat less than our Gray Bussards (*Buteo buteo*) in England, somewhat swifter of wing; and the only good that they do is sometimes to kill the rats." At the time Ligon wrote the greater part of Barbados was still clothed in natural forest, and it is very probable that some species of Buteo was resident. No Buteo has, however, been recorded from the island in recent years.

The "Chicken Hawk" is very common all over St. Vincent and Grenada. It regularly occurs on the northern end of Bequia (north of the Spring estate) where it breeds, and occasionally it visits Mustique. I saw one on Carriacou on August 27, 1904, near the late Mr. John Grant Wells' residence at Hermitage; but as he does not record it from that island it must be a rare straggler there.

This hawk is a great plague to poultry raisers on St. Vincent, but on the other hand is of use to the agriculturist, as it feeds largely on the mole-crickets, which, since the introduction of the mongoose and the consequent killing off of the large ground lizards, have increased to an alarming extent. I once took eighteen of these insects from the stomach and crop of a single hawk. Lister ('**80**, p. 43) says that in the stomachs of all he examined he found the remains of lizards and snakes. In his time, however, the mongoose had not

reached St. Vincent, and reptiles were relatively much more numerous.

Ober gives this bird as occurring on the Grenadines, but this must be a mistake, as except on Bequia and Mustique it is wholly unknown to the natives, nor could I find any trace of it.

In habits this species resembles *B. platypterus*. The nest is rather bulky, and is usually placed in a large tree, often a bread fruit or a cabbage palm. In the spring of 1903 there was a nest in one of these palms in the Botanic gardens at Kingstown, St. Vincent, from which young were successfully raised. The eggs are usually three in number, dull bluish white in color and are (in the six sets which I have examined, in the collection of the late Mr. John Grant Wells, now in the possession of Dr. Dunbar B. B. Hughes of Carriacou) unspotted. I was informed by natives that this bird always lays unspotted eggs.

Pandion haliaetus carolinensis (Gmel.). Sea Hawk; Fish Hawk. — Col. Feilden says of this bird in Barbados: "An irregular and somewhat rare visitor in the fall. Several appeared during the month of October, 1887. One of these is preserved in the collection of Dr. C. J. Manning; another, a female, shot about the same time, is in the possession of Mr. Herbert Hart. An adult male, shot at Graeme Hall swamp on September 28th, 1888, was forwarded to me in the flesh by Dr. Manning."

It occurs regularly as a visitor to St. Vincent, the Grenadines, and Grenada, arriving in August, although stray individuals are sometimes to be met with throughout the year. When I was staying at Chateaubelair, St. Vincent, in October, 1903, there was a single individual of this species that could almost always be found about the mouth of the Richmond River. Mr. Thomas Huckerby, the Wesleyan parson of the district, told me it had been there for about six months. At Union Island, Mr. L. McIntosh showed me the claws of eight or ten of these birds which he had shot there. I met with it myself among the Grenadines at Mustique, Bequia, Union Island, Prune, and Carriacou.

Regerhinus uncinatus (Cass.). Ring-necked Hawk. — This hawk is a resident in Grenada, but is not numerous. It is usually found in the vicinity of the seacoast.

Urubitinga anthracina cancrivora Clark.

Crabier; St. Vincent Black Hawk.

Urubitinga anthracina cancrivora Clark, Proc. biol. soc. Washington, vol. 18, p. 63, Feb. 21, 1905.

Type locality.— Barrouallie, St. Vincent.

Color. — Adult female (type): general color, deep sooty black, the bases of the feathers of occiput, hind neck, and back white, then buff just below the black ends, the buff and white showing through in a sort of irregular mottling; upper and under tail coverts tipped with white, downy feathers of crop region grayish white; malar region dull buff, finely streaked with black; thighs black, the feathers very narrowly tipped with dull rusty. Wings black, the secondaries and tertials mottled and partially banded with dark grayish and rusty, the rusty color predominating on inner webs, the grayish on outer. Bases of primaries mottled with whitish on inner webs; quills also white, forming a grayish white wing spot on under side of closed wing. Tail banded black and white as follows: the feathers mottled at base with white, forming an incomplete whitish band, then a broad black band, another narrow and incomplete white band, a broad black band, then (at about the middle of the tail) a broad white band, followed by a much broader black band and white tips. Shafts of rectrices white at base, becoming black in the first broad black band, and remaining black on upper surface to the end of the tail, but white again on under surface through the broad white central band.

Feet, cere, and base of bill orange; iris brown. Tip of bill black.

This subspecies differs from *U. a. anthracina* in having a longer and relatively narrower bill, with the tip more produced; and in color in having the feathers of the hind neck and back spotted with buff and white (in *U. a. anthracina* the hind neck is spotted with whitish, but there is very little if any on the back), and being in general of a deeper and more sooty black.

Lawrence ('78a, p. 194) remarked that the single specimen sent

up from St. Vincent by Ober did not satisfactorily agree with one in a somewhat similar state of plumage from Mexico. Unfortunately, it was an immature bird.

Mr. J. H. Gurney ('76, p. 487) says that one of these hawks from St. Vincent was living in the Zoological society's gardens in London in 1876. "This example was in immature dress when it arrived in the gardens, but is now in full plumage, with the exception of a slight tinge of rufous brown on the back, and sides of the head, and also on the tertials." He further states that this bird after a moult became slaty or grayish in color, due to a whitish bloom on the feathers, that soon wore off. This condition is comparable to that seen in many birds when in a perfectly fresh condition, and is well brought out in *Caloenas nicobarica* and in the dorsal plumes of *Butorides virescens*.

This large hawk is common in the higher woods of St. Vincent, where it frequents the immediate vicinity of water courses, keeping usually near the ground. It is especially numerous in the woods behind the town of Barrouallie. As it very rarely soars, and is naturally retiring and shy, keeping well away from cultivated areas, it might very well escape the observation of anyone to whom its presence on the island was unknown. The Black Hawk is said by the natives of St. Vincent to subsist entirely upon crabs, and wherever it occurs many little heaps of broken crab shells may be found along the streams. A peculiar fresh-water species (*Geocarcinus ruricola*) which hatches directly from the egg into the adult form, is abundant in the upper reaches of the St. Vincent rivers, has the same local distribution as this bird, and is the species upon which it is said chiefly to feed.

This bird is eaten by the negroes of St. Vincent, and by them is held to be superior to fowl. Its cry is a series of ascending whistling notes, and bears a striking likeness to that of a young turkey, but is, of course, very much louder. In general actions and manner of flight the Black Hawk bears a strong resemblance to the Black Vulture (*Catharista urubu*), but is almost never seen above the tree-tops; when it does soar, however, the similarity is very striking.

Ortalis ruficauda Jard. COCORICO; COCKRICO; GUAN.—The Cocorico is found in the woods on the northern end of Bequia, and on the western end of Union Island, particularly about Chatham

Bay, but it is not so common now as formerly. It was introduced from Tobago.

Numida meleagris Linn. Guinea Fowl. — The "Guinea Bird" is common in a domesticated state in all these islands, and has been allowed to run wild in Balliceaux (Grenadines).

Colinus virginianus (Linn.). Bob-white; Quail.— Schomburgk ('48, p. 681) includes this bird in his list of the birds of Barbados but he is not confirmed by other early writers.

Col. Feilden says that it "is a very rare visitor to Barbados. Dr. Manning has a specimen shot at Bank Hall in St. Michael's parish during September, 1886; the same gentleman saw another in St. James' parish during September, 1887, but did not succeed in shooting it."

Eupsychortyx sonninii (Temm.). Quail (St. Vincent).— This bird was formerly common on Mustique, to which island it was brought by sloops trading between St. Vincent and Venezuela, but is now rare.

Ober is mistaken in giving *Colinus virginianus* from Mustique, as there was never any quail but this on the island. Its habits and notes are like those of the American Quail, and these may have deceived him.

Porzana carolina (Linn.). Sora; Two-penny Chick. — The Sora is a regular fall and winter visitor to these islands, and is found wherever there are swamps. In Barbados it is well known to the natives who call it the "Two-penny Chick" although formerly that name was applied to a grebe.

On St. Vincent it is found in October and November about the mangroves in the vicinity of Arnos Vale and Calliaqua, and I found it on Bequia and Mustique. It is fairly common at Carriacou and on Grenada, and there are specimens in the British museum from Union Island obtained by Mr. G. Whitfield Smith.

Ionornis martinica (Linn.). Cascambiol; Purple Gallinule. — Undoubtedly Hughes (1750, p. 71) refers to this species as the "Blue-pated Coot." He says: "They [Coots or Moor Hens] are distinguished into three kinds; the white [*Fulica caribaea*], — the red [*Gallinula galeata*], — and the blue-pated." They were apparently common on Barbados in his day. At the present time they are only accidental visitors to the island. One was shot by Dr. Manning in the autumn of 1887, and Lieut. Venour of the West

India regiment told Col. Feilden that he saw one captured by some boys with a dog in the swamp below St. Ann's fort in the same month and year.

This bird is rare on St. Vincent, but may sometimes be found in the vicinity of Arnos Vale and Calliaqua. It is common on Grenada and the Grenadines wherever there are swamps. On some of the smaller islands it is very abundant, as at Isle Ronde and Mabouya, where the natives catch it in fish pots baited with corn. They also hunt out and destroy numbers of nests every year, because they say it destroys their growing corn, climbing up the stalks and tearing to pieces the ears.

The nest is placed on the ground in swamps, and is composed of grass and weeds. The eggs are from six to ten, creamy white, finely dotted with umber.

Gallinula galeata (Licht.). Red Seal Coot; Waterfowl; Florida Gallinule. — Col. Feilden says, speaking of Barbados: "Resident. A few still lingered in Graeme Hall swamp in 1888, from whence I obtained a nest with seven eggs in the month of July, when I fully identified the bird. It used to be plentiful at several spots in the island, particularly so at Valentia swamp, and at a pond on the Three Houses estate, but has been exterminated, I think, in those places."

A few of these birds may be found about Calliaqua, St. Vincent, but they are far from common.

On Bequia they are sometimes to be found about the roots of the mangroves on the Spring estate beach. At Mustique they are abundant on the large pond near Mr. Wallace's house. They occur on Canouan, on Mayreau, on the Tobago Keys, on Union Island, and are especially abundant on Carriacou and on Isle Ronde.

On Grenada they are common everywhere among the mangroves, being particularly numerous about Lake Antoine. They are often seen in the harbor of St. George's, about the mangroves in the quiet lagoon across from the town.

The nest is like that of *Ionornis martinica*, and is placed on the ground in swamps. The eggs are from six to ten, light buff spotted with brown.

Fulica caribaea[1] Ridgw. White Seal Coot; Waterfowl;

[1] I have thought it best to refer the Coot of these islands to this form, although no specimens were obtained.

Poule de l'eau.— Col. Feilden records this species as a resident in Barbados as late as 1888. Mr. A. M. McLean told him that about twenty-five years ago the Water Hen and Coot were both abundant at Graeme Hall swamp, and it was no uncommon sight to see twenty or thirty of both species swimming about together in the open water. The cutting down of the brush about Valentia swamp a few years ago banished them from there, and it is probably no longer a resident of the island.

I did not meet with this bird on St. Vincent, but Lister says: "I think this bird is only an accidental visitor to the island. An individual of this species was captured alive in an exhausted condition after a severe gale, in Brabon Bay by a Mr. Nevison, who kindly sent it to me."

On the Grenadines the White Seal Coot is common at Mustique, Mayreau, and Union Island, occurs at Canouan, and is abundant at Carriacou and at Isle Ronde. It is common in all the large swamps on Grenada, and is found on the Grand Etang Lake and on Lake Antoine.

Vanellus vanellus (Linn.). Lapwing.— Col. Feilden writes: "Dr. C. J. Manning has in his aviary a live Lapwing which was shot at and injured in one wing on December 24, 1886, in the island of Barbados. This bird has been in confinement eighteen months when I saw it, and appeared to be quite healthy." Mr. J. H. Fleming (Auk, vol. 18, p. 272, 1901) records this species from the Bahamas.

Squatarola squatarola (Linn.). White-tailed Plover; Black-bellied Plover; Gray Plover; Loggerhead.— Col. Feilden says: "This is a rather rare autumnal visitor (to Barbados), in some years none alighting; it generally arrives after the Golden Plover, toward the close of the shooting season; it hardly ever settles in the pastures, or by the decoy ponds, but on the rocky shores, where it consorts with Ringed Plovers, Turnstones and Sanderlings. I procured a specimen on September 22, 1888." Wells says that small numbers arrive in Carriacou in September and October.

It is recorded from Grenada, but thus far has not been obtained on St. Vincent, although it probably visits that island, as well as most of the Grenadines.

Charadrius dominicus Müll. Golden Plover.— Col. Feilden says: "Stragglers arrive (at Barbados) as early as July and the

beginning of August, but the main flights come with the first heavy weather after August 27, and long experience and observation prove that this date is kept year after year with wonderful accuracy. The course of all the migratory Charadriidae across Barbados in the autumn is from the northwest to southeast, and if the wind blows from the southeast, the birds are brought down to the island, for it appears to be a tolerably well established observation that birds prefer migrating with a 'beam' wind. A shift of wind from the northeast, with squally weather to the southeast, is ardently longed for by the Barbados sportsmen towards the end of August, as this forces the migratory hosts to alight instead of passing over at a great height, as they are seen to do when the wind is from the northeast. The first arrivals of this species are invariably black-breasted birds, showing that the old birds precede the young; and the first comers are nearly all males. The young birds without black on the breast appear about September 12, and continue to pass till the end of October; sometimes stragglers are as late as November. Even in the most favorable seasons, only a fraction of the immense flights that pass over the island ever alight; but if, attracted by the green land and 'mock-birds' pegged out near the shooter's hut, they deviate from their line of flight, they are doomed; for so well do the sportsmen imitate the call of the Golden Plover, and so irresistible is the charm, that the birds come down to it, and, in spite of gaps in their ranks, they wheel round and dash past the shooter again and again till all are killed."

This bird is not abundant on St. Vincent, but is common on the Grenadines and on Grenada, although Wells says the numbers are becoming fewer and fewer every year.

Oxyechus vociferus (Linn.). KILLDEER.— Wells records the Killdeer from Carriacou and from Grenada as a "rare migrant." It is probably casual in all these islands.

Aegialitis semipalmata (Bonap.). RING-NECKED PLOVER.— Common in all these islands, arriving toward the end of August, and remaining until November, frequenting the beaches and pastures, often in company with the smaller sandpipers.

Aegialitis hiaticula (Linn.). RING PLOVER.— Recorded by Col. Feilden from Barbados, one having been obtained by him which was killed at Chancery Lane, September 10, 1888. This is the only record for the species south of Canada on the American side of the Atlantic.

Arenaria interpres (Linn.). Rock Plover; Calico-bird; Turnstone.— Common on all these islands, arriving in August, although individuals may be found at all seasons. They frequent the beaches and the more open parts of the mangrove swamps, running about between the roots of the mangroves after the manner of the Sora (*Porzana carolina*). It is in this latter situation that they are usually met with in spring and summer, when they are remarkably tame.

During the migrations they occur in flocks of sometimes as many as thirty or forty individuals; but in the spring and summer they are usually found in the swamps in companies of five or six.

The adults in the rufous plumage are the first to arrive, while the immature follow in September.

Gallinago delicata (Ord). Wilson's Snipe.— Col. Feilden says that this bird is a regular autumnal visitor, sometimes in considerable numbers, to Barbados. Mr. Massiah has shot as many as ten couples in a day at Chancery Lane, and Col. Feilden has shot them there himself in the months of September, October, and November.

From Hughes' (1750, p. 78) description of the habits of the "Hiding Mopus" and the measurements he gives for that bird it seems probable he refers to this species. The other "Mopuses" appear to be two of the smaller shore birds. The name is not at present applied to any bird at Barbados.

On Grenada and the Grenadines, this is a rather uncommon migrant, arriving in October and November. It frequents the swampy lowlands near the sea.

The Snipe has so far not been recorded from the island of St. Vincent, but it probably occurs there as a rare visitor. The absence of swamps possibly accounts for its never having been obtained there.

Macrorhamphus griseus (Gmel.). Duck-leg; Duck-bill; Dowitcher.— Col. Feilden says: "Though a regular, is somewhat of a rare visitor, appearing along with flights of Yellow Legs (*Totanus flavipes*) in August and September. It is, however, sufficiently numerous to be given a local name by the Barbadian sportsman."

Mr. G. Whitfield Smith has obtained this bird in Grenada and his specimens are now in the British museum.

NOTE.— Probably *M. scolopaceus* also occurs in these islands, although there are no published records. Dr. Sharpe, in the Catalogue of birds in the British museum, does not distinguish between these two birds, but puts all the West Indian specimens under *M. griseus*.

Micropalama himantopus (Bonap.). CUE; STILT SANDPIPER.— Col. Feilden says: "Arrives with the Yellow Legs in July, and continues to pass all through August, and generally into the middle of September, when the flights cease, but stragglers drop in at intervals till October. This bird is easily attracted by the imitation of its call-note, and the flocks are very compact, so that at times many are brought down at one discharge of a gun. They feed on the edges of fresh-water swamps, and do not alight on the dry meadows nor on the sea-beach. The flights only remain on the island a few hours."

This bird visits the Grenadines and Grenada during the migrations, but is not very common. It has not been recorded from St. Vincent.

Tringa canutus Linn. KNOT.— Schomburgk gives this species the local name of "Mopus." It is a rare visitor to Barbados. Dr. Manning ('96, p. 372) in 1886 shot one on December 7, two on the 17th, and three on the 27th. Col. Feilden has one obtained September 6, 1888. It has not been recorded from the other islands.

Actodromas maculata (Vieill.). CHIRP; OCTOBER CHIRP; PECTORAL SANDPIPER. — Col. Feilden writes: "The Pectoral Sandpiper commences to arrive in July and August, increasing in numbers till October, when they usually appear in immense flights; a few stragglers pass over as late as the early part of November. This bird on its arrival in the island frequents flooded and marshy spots where the grass is short, likewise feeding on ploughed lands. The Barbadian sportsmen, many of whom have the most discriminating ear for the notes of the various migratory birds, consider that there is a difference between the notes of the smaller and earlier arrivals, which they designate 'Chirps,' and those of the later arrivals, which are called 'October Chirps'; these are, as a rule, larger and finer looking birds, but I think it is merely that with this species the immature precede the adult on the southward migration. Mr. Massiah has drawn my attention to a habit of this bird which I have not previously seen noticed; when reaching the ground and alighting from passage, all the individuals in the flight

throw themselves on the ground with their breasts touching it, in the position of a brooding hen, or pigeon on eggs. Has this habit anything to do with its trivial name of Pectoral Sandpiper?"

The difference in size between the sexes in this bird is frequently considerable (*vide* Sharpe, Cat. birds Brit. mus., vol. 24, p. 562, 1896), the female averaging about three quarters of an inch less than the male in length, while in the large series collected by Mr. John Murdoch at Point Barrow, Alaska (*vide* Lieut. Ray's Report of the expedition, p. 111, 1885), "the smallest female was fully an inch and a half shorter than the longest male." From this it would appear that the females take precedence over the males in the migrations, and not the young over the adults. It has been noticed in New England (*vide* Auk, vol. 16, p. 179, 1899) that the smaller birds are the first to arrive in any given locality, while the larger ones appear a week or so after.

The Pectoral Sandpiper is abundant on Grenada and the Grenadines during the migrations, and is fairly common on St. Vincent.

Actodromas fuscicollis (Vieill.). Gray Nit; White-rumped Sandpiper. — Col. Feilden says: "Arrives in July and continues on the island (Barbados) till the end of November, receiving additions to its numbers. It flies in company with *E. pusillus* and *A. minutilla*, and I have brought all three down at one shot."

There is a specimen in the British museum from St. Vincent, obtained by Mr. G. Whitfield Smith, but otherwise it has not been obtained in these islands, except at Barbados, although it is probably a rather common migrant.

Actodromas minutilla (Vieill.). Cockroach Nit; Least Sandpiper. — Common on Barbados from the middle of July till the end of October. It occurs on all the other islands, but not in such numbers as at Barbados.

Erolia ferruginea (Brünn.). Curlew Sandpiper. — Wells says that small numbers of the Curlew Sandpiper arrive in Carriacou in September and October. He also records it from Grenada.

Ereunetes pusillus (Linn.). Grass Nit; Semipalmated Sandpiper. — Everywhere abundant in these islands, arriving about the middle of July and remaining till November.

Calidris arenaria (Linn.). Sandy Snipe; Sanderling. — Occurs throughout these islands, frequenting the beaches in little companies; arrives in August, but is never very abundant.

Limosa fedoa (Linn.). Marbled Godwit. — Wells records the Marbled Godwit as a rare migrant on Grenada and Carriacou, one or two arriving with the first flights of Yellow-legs (*Totanus flavipes*).

Limosa haemastica (Linn.). Hudsonian Godwit. — Col. Feilden says: "An annual visitor (to Barbados), in some years far more numerous than in others, generally arriving in October. Mr. Massiah informed me that he has a note that on October 10, 1878, this species passed over the island in large and continuous flocks the whole day. I have an example in my collection, a male, shot at Graeme Hall swamp by Mr. Herbert Hart on October 6, 1888."

Totanus melanoleucus (Gmel.). Pika; Greater Yellow-legs. — Col. Feilden says: "This bird arrives as early as May; I have a note of their having been seen at Graeme Hall swamp on May 5, 1888 (*fide* C. Manning), but the main flights occur during September and October, arrivals continuing in diminished numbers till the middle of November. It appears in comparatively small parties, a flock of twelve or fifteen being considered a large flight."

The Pika is common on St. Vincent, Grenada, and the Grenadines during the migrations. The British museum has specimens from Union Island, Grenada, and St. Vincent, collected by Mr. G. Whitfield Smith.

Totanus flavipes (Gmel.). Long-legs; Yellow-legs.— Abundant on all these islands, arriving about the middle of July. On the Grenadines a few may be found in the swamps throughout the year.

On October 2, 1903, I saw one of these birds flying about inside the "new crater" of the St. Vincent Soufrière. What it was doing up there 4000 feet above the sea is hard to imagine even though in its present state the floor of the "new crater" does somewhat resemble a beach. This was the only bird seen on the volcano with the exception of a few martins (*Progne dominicensis*) near its base.

Helodromas solitarius (Wils.). Black-back; Solitary Sandpiper.— Common on Barbados, St. Vincent, and the Grenadines from July till December. It is found singly or in pairs, sometimes in little parties in favorable localities. If a party of these birds be started, the individuals fly away independently of each

other, or in pairs, just as they do in the north. On Grenada and St. Vincent it is usually found along the rivers, but does not ascend them so high as does *Actitis macularia*. On Barbados this is not reckoned a game bird, and is not hung up with the other shore birds after a day's shooting, as it is supposed to spoil them. This is probably due to its strong and rather disagreeable odor.

Pavoncella pugnax (Linn.). RUFF.— Schomburgk ('48, p. 681), says: "The Ruff Sandpiper is a British bird, and I have been informed that it is the first time that this species has been recorded as having been found on the other side of the Atlantic. Mr. Bishop sent it to me among other migrating birds, and observed that its name was not known, from which I infer that its occurrence in Barbados is a singular circumstance."

Col. Feilden obtained another specimen of this bird in full breeding plumage from Mr. H. Alleyne, which was shot by Mr. H. Simson of Bridgetown in Graeme Hall swamp in 1878.

Symphemia semipalmata (Gmel.). WHITE-TAILED CURLEW; WILLET.— A regular, but rather uncommon visitor. I saw one at Chateaubelair, St. Vincent, in October, 1903, and it is recorded from Barbados, Carriacou, and Grenada.

Bartramia longicauda (Bechst.). COTTON-TREE PLOVER.— Col. Feilden says: "Generally arrives (in Barbados) about the middle of August, and a few remain until March. On arrival the flocks break up and scatter over the grass-lands, corn-fields, yam and sweet-potato patches, feeding on grasshoppers, beetles, and other insects. They are not attracted by the 'mock-birds,' neither do they respond to the whistle of the sportsman. They run as fast as a Guinea fowl, and generally rise well out of shot. Their note is peculiarly pretty, a soft liquid cry. The local name given to this bird took its origin from its habit of frequenting the cotton fields when this plant was cultivated in Barbados."[1]

Wells says that small numbers arrive in Grenada and Carriacou during September and October. They are very wary, and frequent the hilly pastures. It has not been recorded from St. Vincent.

The Upland Plover is becoming more and more scarce every year, according to the natives in these islands.

[1] Hughes' "Cotton Tree Bird," however (**1750**, p. 72), is evidently a Passerine. *Vide* Hypothetical species, "The Cotton-Tree Bird."

Tryngites subruficollis (Vieill.). Buff-breasted Sandpiper.— This bird is recorded as a rare visitor to Barbados. Col. Feilden has one obtained in the autumn of 1887, another on October 6, 1888, and a third about the year 1847.

Actitis macularia (Linn.). Spotted Wag; Spotted Sandpiper.— Abundant throughout these islands, many remaining all the year. On Barbados it is especially common along the streams in the Scotland district. On Grenada and St. Vincent it follows up the water courses into the mountains, to the borders of the high woods and even beyond.

Numenius hudsonicus Lath. Crook-billed Curlew; Woodcock; Hudsonian Curlew.— Rather uncommon, though regular migrant, arriving in the early part of August. It has not yet been recorded from St. Vincent.

Numenius borealis (Forst.). Chittering Curlew; Eskimo Curlew.— Col. Feilden says: "Arrives about the end of August, but passes more frequently in September. The first I obtained in 1888 was on September 5, when immense numbers passed over the island, though comparatively few alighted. The same day great flocks of Golden Plover (*Charadrius dominicus*) and Long Legs (*Totanus flavipes*) arrived. I saw over a hundred of each of these species shot at one stand by a single gun." Hughes (**1750**, p. 77) says: "These, as well as most Curlieus, often come in great flocks. They are next in bigness to the Crooked-billed Curlieu." Both Hughes and Schomburgk ('**48**, p. 681) give this bird the local name of "Shivering Curlew."

Wells says that at Carriacou and Grenada this curlew comes in with the plovers, but remains only a few days. On September 5, 1904, I saw two birds of this species on a mudflat near Harvey Vale, Carriacou, in company with great numbers of Yellow-legs (*T. flavipes*). These were the only examples I met with during my entire stay in the West Indies.

The Eskimo Curlew has never been recorded from St. Vincent although it doubtless occurs there.

Recurvirostra americana Gmel. American Avocet.— Col. Feilden says that Mr. Massiah informed him that he shot an Avocet at Valentia swamp in the autumn of 1880, and Mr. I. Tingling shot another on October 1, 1888, at Finney's Hill, St. Philip's, Barbados.

Himantopus mexicanus (Müll.). Black-necked Stilt.—

Col. Feilden says, speaking of this bird on Barbados: "A rare visitor, though seldom a year passes without one being shot at Graeme Hall swamp. Mr. I. Tingling informed me that he saw one there in the autumn of 1887, and another on September 17, 1888."

Ober obtained this bird on St. Vincent, and there is an adult female in the British museum collection procured by Mr. G. Whitfield Smith on that island in 1889.

Stercorarius crepidatus (Gmel.). Jaeger.— An adult female of this species with enlarged ovaries was brought to Col. Feilden alive on July 10, 1888, at Barbados. It had been caught by a fisherman with a hand-net. The bird was rather thin, but not emaciated.

Mr. M. J. Nicoll observed a bird of this species between St. Vincent and Carriacou on January 27, 1904. There are no other records.

Larus atricilla Linn. Mauve; Laughing Gull.— Specimens of this species from these islands are somewhat smaller than others from more northern points in its range; but as in many gulls, birds from the north average larger than examples from more southern localities. I have not considered it advisable to give it a subspecific name.

The Laughing Gull is casual on Barbados. Col. Feilden has a specimen shot by Dr. Manning in the summer of 1887, and another killed on July 24, 1888.

This bird is common along the shores of St. Vincent and Grenada, but in the former island is mainly confined to the Kingstown district. In Grenada one or two may usually be seen flying about the docks and wharves of St. George's.

In the Grenadines the Laughing Gull is common everywhere, particularly so about Carriacou, where it is seen in flocks of twenty or thirty. Wherever pelicans are feeding there are usually to be found a few birds of this species, watching for a chance to get a share of the larger birds' meal, which they do by alighting on the latters' heads and reaching down into their beaks.

At Carriacou after a rain these birds frequent the pastures in numbers, particularly at Beausejour and Harvey Vale. They nest on the small islets about Carriacou, and rather generally on the more isolated keys all through the Grenadines.

The eggs are three, sometimes four, dark buff, with blotches of brown, that sometimes form a ring about the larger end.

Measurements.

Sex.	Locality.	Wing. mm.	Tail. mm.	Culmen. mm.	Depth of Bill. mm.	Tarsus. mm.
♂	Union Island, Grenadines	293	120	37	11	43
♂	" " "	300	120	37	10	44
♂	St. Mary's, Ga.	345	130	42	12	53
♂	" "	343	141	40	12	52
♂	Little Gaulding Key, Bahamas	315	120	38	12	47
♂	Anastasia Island, Fla.	350	130	42	12	50

Gelochelidon nilotica (Hasselq.). Gull-billed Tern. — This is a rare visitor to these islands. Col. Feilden obtained two specimens at Barbados, one killed October 6, 1888, and the other on the following day. There are no other records.

Sterna maxima Bodd. Royal Tern. — The Royal Tern is found rather sparingly along the leeward coast of St. Vincent, throughout the Grenadines, and about Grenada, being rather more numerous about Barrouallie in St. Vincent, the Tobago Keys and the southern part of Carriacou in the Grenadines, and Grenville in Grenada, than at other points.

The eggs are three in number, laid on the ground in sandy places; white or greenish buff in color, blotched with brown of different shades, especially toward the larger end.

Sterna dougalli gracilis (Gould). Carrect; Roseate Tern. — The resident West Indian Roseate Terns appear to have the bill with more or less red at the base instead of wholly black as in more northern birds, so I have referred them provisionally to Gould's *S. gracilis*. Mr. Saunders (Proc. zool soc. London, p. 652, 1876) gives an interesting account of the variations in the color of the bill in this species, and says that all the birds he has seen with the red bill have been from tropical localities. Gould's type came from Australia.

The Roseate Tern is seen rather rarely about the leeward coast of St. Vincent, but is more common about Grenada. It is of fairly common occurrence in the Grenadines, breeding, among other places, at Frigate Island and Rose Rock near Carriacou. Formerly it bred in numbers at Isle Jaques Adam near the town of Hillsborough, but for some reason has of late years deserted this locality.

The nest is made on the ground in sandy places. It is composed of sticks, dry weeds, etc. The eggs are three or four, varying from

white to deep brown in color, spotted and blotched with dark brown of various shades.

NOTE. — Probably *S. dougalli dougalli* should have a place in the avifauna of these islands as a winter visitor from North America. Mr. Cory has specimens taken in Guadeloupe in September which have the bill wholly black, while others in his collection, taken near Antigua in June and July have the base of the bill red for from one third to one half its length.

Sterna antillarum (Less.). LEAST TERN. — One specimen of the Least Tern was obtained at Chancery Lane, Barbados, on September 8, 1888, and another on October 17, of the same year. There are no other records.

Sterna fuliginosa (Gmel.). TWAROO; HURRICANE-BIRD; SOOTY TERN. — The Sooty Tern is common at sea in medium sized or large flocks in this part of the Caribbean, especially in the channel between St. Vincent and St. Lucia, and between these islands and Barbados. It is occasionally seen along the leeward coast of St. Vincent, usually singly, and small flocks are often to be met with between Bequia and Canouan. It is abundant in the southern Grenadines, from Carriacou to Grenada, breeding on Isle Ronde, Kick-'em-Jenny, Lee Rocks, Bonaparte Rocks, and Isle de Large, as well as on some of the smaller islets.

Although abundant within sight of Barbados, it has never been known to visit that island.

The single egg is placed on the ground, usually in sandy spots, and is white, blotched with reddish brown and lilac.

Sterna anaethetus (Scop.). BRIDLED TERN. — This species is common about the southern Grenadines, nesting abundantly at Lee Rocks, and on Rose Rock. There are also smaller colonies on many other of the smaller keys, and a number breed on White Island, in the midst of a rookery of several hundred Noddies (*Anous stolidus*). Single birds or pairs are frequent in the northern Grenadines and about the shores of St. Vincent and Grenada. I have seen it a few miles off the coast of Barbados when out in a flying-fish boat, but it has never been seen or taken in the immediate vicinity of that island.

The egg of this species is placed on the ground, and is creamy white, spotted and blotched with reddish brown and umber, especially toward the larger end.

Hydrochelidon leucoptera (Meisn. and Schom.). WHITE-WINGED BLACK TERN.— One specimen of this bird was obtained by Col. Feilden on October 24, 1888.

Hydrochelidon hybrida (Pallas). WHISKERED TERN.— There is a mounted specimen of this species in the British museum marked "Barbados" presented by Sir Robert H. Schomburgk. He does not, however, include it in his list of the birds of that island (*vide* Saunders, in Yarrell's British birds, 4th ed., vol. 3, p. 529, 1884; Cat. birds Brit. mus., vol. 25, p. 10, 1895).

Anous stolidus (Linn.). MWEN; NODDY.— The Noddy is common among the Grenadines, nesting at Isle de Large, Rose Rock, and White Island near Carriacou, and on Western Key off Bequia. There are also other less important breeding places. This bird is often seen at sea about these islands, and sometimes visits the coasts of St. Vincent and Grenada, particularly the windward coast of the latter island. I have met with it within a few miles of Barbados when out in a flying-fish boat, but it has never been taken there, nor seen near the shore.

The flight of this species is different from that of other terns, reminding one of the flight of the boobies (Sula).

The nests are placed on low bushes or trees, sometimes on the ground. The single egg is grayish yellow, spotted and blotched with reddish brown and lilac.

Columba squamosa Bonn. RAMIER.— Sir Hans Sloane in his Natural history of Jamaica (**1707**, vol. 1, p. 34) says, speaking of Barbados, that "Turner (ap. Purchas. p. 1265) found Hogs, Pigeons, and Parrots there."

Hughes (**1750**, p. 76), says, speaking of "The Wild Wood Pigeon": "This is about the bigness of an House Pigeon.

"The head is of a blackish color; and from the under bill to the breast, of a light mouse color; from thence to the belly and the under part of the tail, of an ash color; the upper side of the neck, back, and wings, of a dark ash color, growing lighter toward the extremities of the wings.

"These come hither, tho' in no great numbers, about the latter end of July or August, always alighting upon trees, and feeding upon the berries of them."

These references must refer to this species; Hughes' description of the color is rather inexact, but was perhaps taken from memory;

his note of the size is very close, and he noticed the exclusively arboreal habits of the birds. There is no other pigeon or dove of this nature which could reasonably be supposed to have been an annual visitor to Barbados.

The Ramier is not rare in the high woods of St. Vincent (to which part of the island it is confined), and is common at the higher altitudes of Grenada and on all the Grenadines. On these latter islands it occurs at all points, even among the low bushes along the seashore. Ramier are particularly abundant on Prune Island, the Tobago Keys, the western end of Petit Martinique, and on Church Rock, between Battowia and Balliceaux. Their numbers have of late years seriously diminished on the small islands, probably on account of their not being given sufficient protection during the breeding season. They nest from the latter part of May until August, mostly on the smaller keys. After the breeding season they disappear almost entirely from the Grenadines, but return the following May.

This is the chief game bird of these islands, and is much hunted. The flight is rapid and powerful, and the birds regularly cross over from one island to another to feed, returning at night to roost on the smaller keys. Formerly numbers could be shot any evening about four o'clock from Clifton House, Union Island, as they flew from that island over to Prune to spend the night. They could be obtained at Hermitage House, Carriacou, in the same manner, as they flew past, going to one or other of the small keys near by.

Dr. Dunbar B. B. Hughes, the district medical officer at Carriacou, told me that in the spring of 1904 he shot a pure white bird of this species on one of the small islets near that island. At about the same time there was another, largely mixed with white, on Canouan, but it was very wary and nobody succeeded in killing it.

During the recent eruptions of the Soufrière on St. Vincent, large flocks of Ramier visited Grenada, probably from that island, but subsequently disappeared.

The nest is a loose structure, usually placed rather high. The eggs are two, white, much like those of the Domestic Pigeon.

Zenaida zenaida aurita (Temm.). Wood Dove; Bequia Dove; Tourterelle; Seaside Dove.—The Wood Dove is common on Barbados in places where it is accorded protection, notably in the grounds of Codrington college, the grounds of Gov-

ernment house, and about Mr. James H. Inniss' residence, Grazettes. At other points it is not abundant, and is very shy.

This bird is not a resident at St. Vincent, but a few of them stray over from the northern Grenadines, especially in the spring, visiting the district about Calliaqua and Arnos Vale. The natives recognize the fact that this species is not a resident, but occurs commonly on the neighboring islands as such, and hence apply to it the name of "Bequia Dove," in somewhat the same way that they call the Holoquiscalus of St. Vincent the "Bequia Sweet."

On the Grenadines it is abundant, and may often be seen over the sea, passing from one island to another, or from the northern Grenadines to St. Vincent. It breeds on all the islands and keys, and is especially numerous on Battowia, Balliceaux, Mustique, the Tobago Keys, and Prune. Although a lowland species, it occurs at all points in the smaller islands.

On Grenada it is common all along the coast, especially toward the southern end of the island, but is rarely found far from the sea. It frequents mainly the open pastures and sea cliffs.

One specimen, obtained at Barbados, had a single white feather near the middle of the back.

The nest is a loosely constructed affair, like that of *Zenaidura macroura*, placed in trees or bushes. The eggs are two, white.

Zenaida vinaceorufa Ridgw. Trinidad Ground Dove.—Lawrence ('85) separated the bird from Grenada and Carriacou, giving it the name of *Z. rubripes*, but later writers have not followed him. Von Berlepsch ('92) says: "Eine sorgfältige Vergleichung dieses Curaçao-Vogels mit einen Serie von 10 auf der Insel Carriacou (Grenadinen) von Herrn. J. Grant Wells gesammelten Exemplaren — welche als Typen zu *Z. rubripes* Lawr. zu betrachten sind — hat mich davon überzeugt, das *Z. rubripes* mit *Z. vinaceorufa* Ridgw. zusammen fällt. Ebenso wenig vermag ich einen Trinidad-Vogel sowie ein ♂ von Suonga, British Guiana (Coll. Whitely), von der typischen *Z. vinaceorufa* Ridgw. aus Curaçao zu unterscheiden."

Lawrence says, quoting Wells, in the article containing the original description, that this is not a common bird on Grenada. Several specimens were obtained on Glover's Island, where Wells thinks they resort during the nesting period, and one (type of *Z. rubripes*) on Grenada proper.

On Carriacou this species was formerly abundant but is now on the decrease. It is only found about the southwestern end of the island, especially on the Harvey Vale and Beausejour pastures. On July 12, 1904, I found a number (perhaps a dozen pairs) at the latter place and obtained four, but did not again meet with it, although I searched carefully in its favorite haunts. It is said to occur mainly in the summer, appearing in July, and is locally supposed to come from the mainland and from Trinidad, as does the Fork-tailed Kingbird (*Muscivora tyrannus*); hence its local name. It nests sparingly on Carriacou, and on the smaller islets off the coast.

In habits it much resembles *Zenaidura macroura*. The loosely constructed nest is placed in low trees; the eggs are two, white.

Engyptila wellsi Lawr. Pea Dove. — This species is confined to the island of Grenada and to the islets just off the coast, on some of which it is very numerous.

Columbigallina passerina trochila (Bonap.). Ground Dove; Ortolan. — This bird is common on Barbados, especially in the pastures near the seacoast. It was more abundant formerly before the introduction of the mongoose. Col. Feilden states that he has heard of as many as fifty couples being shot in a day by two guns; this could hardly be accomplished now.

On St. Vincent the Ground Dove is not at all abundant. The only places where it can be seen at all commonly are the Kingstown valley and the neighboring windward district. It keeps near the seacoast, never venturing far into the hills.

On Grenada it is found in numbers about the southern end of the island, and is fairly common at other points, keeping, however, near the sea. As on the other islands, the mongoose has made serious inroads into its ranks.

On the Grenadines, where the mongoose does not exist, it is abundant, except on some of the smaller keys, notably Prune, where it is rare.

On Barbados and St. Vincent the negroes catch numbers of these birds in traps and "springes," the latter being supple twigs bent into a spiral form and secured in that position with twine, from which, as well as from the twig, horsehair nooses project upward. The bait is placed on the ground underneath.

The nests are placed on the ground in tufts of grass, in bushes,

or in trees, sometimes as much as ten feet from the ground. The two eggs are white.

Geotrygon montana (Linn.). PERDRIX. — Formerly common in the higher parts of St. Vincent and Grenada, but now probably extirpated from the former island, and very rare on the latter. It is essentially a ground species, thereby falling an easy prey to the mongoose.

Wells says that the nests are usually placed near the ground in trees or on stumps, very often in a tree fern; the eggs are two, light coffee-color, one usually darker than the other.

Coccyzus minor minor (Gmel.). CUCKOO MANIOC; RAIN-BIRD. — On examining a series of thirty-eight specimens of *Coccyzus minor* from the islands of Dominica, St. Lucia, St. Vincent, the Grenadines, and Grenada, I find that there are three forms apparently well worthy of recognition.

The bird from Dominica has been named *Coccyzus minor dominicae* by Captain Shelley (Cat. birds Brit. mus., vol. 19, p. 306, 1891), and is characterized as having a larger and thicker bill than *C. m. minor*, and in being darker, especially below. Mr. Riley (: 04b, p. 285) has renamed this form *C. m. shelleyi*, believing the name *dominicae* to be too close to *dominicus*, given (*Cuculus dominicus*) by Linnaeus (Syst. nat., vol. 1, p. 170, 1766) to the resident West Indian Yellow-billed Cuckoo (*C. americanus*); but it seems to me that the two terms *dominicus* and *dominicae* are sufficiently distinct, and no change in nomenclature is called for, although it certainly would have been better had Captain Shelley chosen some other designation for his new bird.

The series of 19 specimens of this species from the Grenadines and 4 from Grenada collected by myself shows that the birds from these localities are identical, there being no difference between those from Grenada and those from the smaller islands. Mr. Riley (*loc. cit.*) includes Grenada in the habitat of *C. m. dominicae*, and gives the measurements of a specimen from that island which certainly is not the form I obtained there. All my birds were taken in the vicinity of Point Saline, near the southern end of the island, on low-lying ground, open, or grown up to scrubby bushes and cactus, just such conditions as obtain on the Grenadines. The larger part of the island, however, is damp and more or less wooded resembling in this respect Dominica, St. Lucia, or St. Vincent; and

it is very possible that there are two forms here, one inhabiting the hot and dry lowlands in the southern part of the island, and the other the moist wooded regions. Unfortunately, I have not been able to obtain a specimen of true *C. m. minor* from South America [1] for comparison with my birds from Grenada and the Grenadines, but I have thought it best to refer them to this form, as they agree fairly well with Buffon's plate. In color they are pale below especially on the throat and breast. Compared with an example of *C. m. nesiotes* from Jamaica, while only slightly paler on the abdomen, they are strikingly less buffy on the throat and breast, which are almost a dead white tinged with gray (more pronounced in the males) particularly along the sides of the neck. The bill is small and weak in comparison with that of St. Vincent birds.

The Cuckoo Manioc is common on all the Grenadines. It is slow and stupid in its actions, and frequents hillsides grown up to scrub, although it is sometimes found on the borders of mangrove swamps. Its cry is a peculiar guttural rattle, sounding in the distance like the noise made by the American marsh frog (*Rana palustris*).

On Grenada this bird is uncommon, and appears to be mainly confined to the low scrubby districts in the vicinity of Point Saline, where the conditions are similar to those on the Grenadines.

The nest is loosely built, like that of *C. americanus*, and generally well hidden. The eggs are two or three in number, pale green.

The Mangrove Cuckoos which I obtained on St. Vincent appear to represent a well marked local race, for which I propose the name

Coccyzus minor vincentis subsp. nov.

St. Vincent Cuckoo.

Coccyzus minor Lawr., Proc. U. S. nat. mus., vol. 1, p. 193, 1878; Lister, Ibis, 1880, p. 41; [Clark], W. I. bull., vol. 5, p. 88, [1902]. (Part.)

Coccyzus minor dominicae Shelley, Cat. birds Brit. mus., vol. 19, p. 306, 1891; Cory, Cat. W. I. birds, pp. 102, 141, 1892; Mayn., Cat. birds W. I., 2d app., p. 36. no. 76. 1, 1903. (Part.)

Coccyzus minor shelleyi Riley, Smiths. misc. coll., vol. 47, p. 285, 1904. (Part.)

[1] The type locality of *C. minor* is Cayenne.

Type.— No. 12,796, ♂ ad., coll. E. A. and O. Bangs. Peter's Hope, St. Vincent, Feb. 11, 1904.

This form resembles *C. m. dominicae* from Dominica, but is paler below, and has a longer and stouter bill. The color of the underparts is intermediate between that of *C. m. dominicae* and *C. m. minor* from the Grenadines, but the bill is considerably larger than in either.

Mr. Riley includes the St. Vincent Cuckoo under *C. m. dominicae*, but appears to have had no specimens for comparison. None of the six Dominican birds which I have examined shows any approach to this light-colored, large-billed form.

Mr. Nicoll (:04, p. 565), speaking of the Mangrove Cuckoos of St. Vincent, says that they are apparently intermediate between *C. m. minor* and *C. m. maynardi*; but he himself obtained no specimens on the island, and his statements are based on birds in the British museum collection. The two examples which I took, as well as others which I saw, were intermediate between *C. m. minor* and *C. m. dominicae* in color. Mr. Nicoll's observations would, however, be applicable to birds from the Grenadines in a rather worn state of plumage, or to specimens in a faded condition from those islands; and, in view of the rarity of this bird on St. Vincent, and the abundance of *C. m. minor* on the Grenadines, it is very possible that the examples examined by Mr. Nicoll from "St. Vincent" were in reality of Grenadine origin.

Unfortunately for ornithology, the colony of St. Vincent includes not only the island ("mainland") of that name, but also all the Grenadines north of Carriacou. Now St. Vincent proper and the Grenadines, as pointed out, lie in different faunal areas, and unless one can be absolutely certain where a specimen was taken, it is unsafe to admit it into consideration. The Grenadine towns are locally regarded simply as country villages of St. Vincent, just as much as Georgetown, Layou, Chateaubelair, or Barrouallie on the island itself. To give an idea of the confusion which might arise: *Ortalis ruficauda* is found only on Bequia and Union Island, and *Eupsychortyx sonninii* occurs only on Mustique, but all these islands are politically "St. Vincent." Moreover, *Coccyzus minor* (*minor*), *Holoquiscalus luminosus*, and the Yellow-breast, *Coereba wellsi* (form *morrisi*) are abundant on all the Grenadines, while the corresponding forms, *C. minor* (*vincentis*), *H. dispar*, and *C. atrata*

(form *saccharina*) occur only on the island of St. Vincent, and are all very rare. Therefore, unless it can be proved that specimens of Mangrove Cuckoos, blackbirds, or Yellow-breasted Honey Creepers could not by any chance have been procured on Bequia (only six miles from Kingstown) such specimens must be disregarded in considering the avifauna of this district.

On the Grenadines, the plumage of birds fades with remarkable rapidity, owing to the small rainfall and general absence of trees, and the consequently dry, hot, and unsheltered conditions under which the birds live. This fading is very noticeable in the Mangrove Cuckoo, and it is unsafe to draw any conclusions from any but perfectly fresh material.

Measurements.

Sex.		Locality.	Wing. mm.	Tail. mm.	Culmen. mm.	Depth of Bill. mm.
♂	*C. m. vincentis* (type)	St. Vincent	137	177	30	12
♀	" (topotype)	"	137	176	31	12
—	" (average of four)	St. Lucia	139	178	28	11
♂	*C. m. dominicae* (average of three)	Dominica	143	166	28	11
♀	" " " "	"	143	167	28	11
♂	*C. m. minor* (average of three)	Bequia	134	176	27	11
♀	"	"	130	173	25	10
♂	" (average of eight)	Union Island	133	169	27	10.5
♀	" (average of three)	" "	133	168	26.5	10
♂	" (average of two)	Carriacou	134	167.5	26.5	10
♀	"	"	132	176	27	11
♂	" (average of two)	Grenada	133	173	27	10
♀	" " " "	"	132	172	28	11

The seven specimens examined from St. Lucia all agree in color with the St. Vincent birds, but approach those from Dominica in the character of the bill. Only the two having the largest and the two having the smallest bills were measured.

The Cuckoo Manioc is rare on St. Vincent at present. I met with several in the upper part of the Peter's Hope valley, near Barrouallie, and saw single individuals in the woods behind Chateaubelair (October, 1903), on Belleisle Hill (February, 1904), and in the grounds of the Agricultural school at Kingstown (February, 1904).

Lister remarks that he has often heard its notes when entering the high woods, although he mentions that it also occurs in the lowlands. It appears to be now confined to the borders of the high woods and to clearings in the higher mountain valleys.

Coccyzus americanus (Linn.). YELLOW-BILLED CUCKOO.— Col. Feilden records the capture of a male of this species at Graeme Hall swamp, Barbados, on October 6, 1888.

Wells saw a pair at Grand Anse pasture, Carriacou, in 1896, one of which, a male, he obtained, and since then has found them every year.

I shot a male on the Spring estate pasture, Bequia, on November 30, 1903.

It has never been obtained on St. Vincent or Grenada, but probably occurs as a rather rare winter visitor; Mr. Cory gives it from Barbuda, and Mr. Chapman obtained one on Trinidad.

Crotophaga ani Linn. TICK-BIRD; CHAPMAN-BIRD; CORBEAU. — The Ani is common on St. Vincent about the cleared land. It is said to have been introduced into the island from Tobago in the sixties by a Mr. Chapman, by whose name it is now commonly known.

On Grenada it is very numerous. Among the Grenadines it occurs on the southern end of Bequia (Friendship estate), on Mustique, Canouan, Union Island, Petit Martinique, and Isle Ronde, but is absent from the other islands.

The nest of this species is a bulky structure of sticks and dry leaves, placed in a tree or bush, usually rather low. Several pairs use the same nest, all the females laying their eggs in it. Sometimes three or four may be seen sitting on the nest at one time. The eggs are green, covered with a white calcareous deposit, through which the ground color shows faintly.

Amazona guildingii (Vig.). ST. VINCENT PARROT.— In view of the rarity of this bird in collections, and considering the fact that nothing has been written on the variations in its plumage, nor on its young stages, I have thought it best to go somewhat into detail in regard to its coloration. I obtained eight specimens, no two of which are exactly alike in either measurements or plumage.

Color.— Adult:[1] "Orange brown, edges of feathers black; pileum white, turning to yellow on the hind part; lores and feathers under the eye, white. Occiput, throat, and sides of head, blue, with bases of feathers yellowish green; lower part of the neck more or less tinged with green; the feathers of the abdomen green near the

[1] Salvadori, Cat. birds Brit. mus., vol. 20, p. 273, 1891.

black edges. Under tail coverts green yellow; spurious wing and primary coverts green, the first with a bluish tinge, the last orange at the base of the outer ends. An orange wing speculum at the base of the first three or four secondaries; primaries black, with their bases yellow; secondaries blue, edged with green, the first three or four with the bases of the outer webs orange, forming the wing speculum. Bases of the inner secondaries yellow; tertials partly green; upper part of the metacarpal edge, yellow orange, the lower part green, with the edges of the feathers blue; smaller under wing coverts orange, mixed with green, greater ones and bases of the inner webs of the quills, yellow; tail above, yellow and orange at the base, blue in the middle, and yellow at the tip; below, orange at the base, yellow at tip, green in the middle; bill pale horn, tarsus gray."

In fresh specimens the iris is orange, the feet light bluish gray, the naked skin about the face and eyes grayish at base of bill, becoming bright blue behind; bill light bluish gray at base, becoming ivory-white at tip. In some specimens the skin of the face was much brighter than in others, and was brighter in the brown birds.

No. 1 (immature): general color above dull greenish brown, becoming brighter green on rump. Breast brown, becoming green on abdomen. Under surface of quills green (instead of yellow) with only a tinge of yellow at the base. The orange speculum on the secondaries is present, but there is no yellow on the primaries. Tail yellow at base, becoming orange near the central band, this color extending into the band in the shape of an inverted V on each feather. The central band is green, becoming blue distally. Tip of tail orange, the extremity of each feather greenish yellow. Hind head, throat, neck, and sides of head, forward to over eye, blue. Pileum and lores clear white; occiput orange.

No. 2: resembles no. 1, but the head is brighter in color, with less blue. The feathers under the eyes are light orange, tipped with blue, and the general coloration is somewhat browner. There is no yellow on the primaries. The tips of the tail feathers are yellow, becoming orange on the inner webs of all but the central pair.

No. 3: back dull orange brown, tinged with green, becoming dark chestnut on rump. Greater wing coverts orange brown; lesser under wing coverts bright yellow, tipped with black. Basal half of primaries yellow, forming a large yellow patch on extended

wing, continuous with the orange wing speculum. Bend of wing brown, green, and orange. Distinct collar about neck, green. Pileum dirty white, tinged with grayish blue, becoming more strongly blue toward occiput. The bases of the feathers are orange, this color encroaching more and more on the feathers posteriorly. Feathers under eye, yellow at base, green and blue at tip. Occiput blue, the feathers being orange at the base, then green, tipped with blue and edged with black. Feathers of throat orange, tipped with blue. Basal portion of tail yellow, becoming distally deep orange red; central band, the basal half green, the distal blue; tip orange, becoming greenish at the extremity.

No. 4: In general brighter and browner than no. 3; the pileum is clearer white, becoming orange on occiput. Feathers under eyes orange, tipped with white. There is very little blue on the hind head and neck, but there is a distinct green collar. The rump is brighter than in no. 3, becoming orange brown on upper tail coverts.

These are the most distinct color types represented. The main differences between the immature and the adult seem to be that the former are dull brownish green, brightest and greenest on the rump and abdomen, duller on the head, the pileum being suffused with gray, and with the primaries entirely green. In life the difference between these two types of plumage is very noticeable. The adults seen against a background of tropical foliage appear decidedly yellow, with the middle third of the wing basally orange, and distally yellow, and the wing entirely yellow underneath. The young appear green, with only a small patch of orange on the wing. When a pair, one of the yellow type of coloration and the other of the green, are seen flying together, as they often are, the difference is much more striking than in the prepared specimens; so much so, in fact, that it is a rather prevalent idea on St. Vincent that there are two species of parrots on the island.

Measurements in Millimeters.

	?[1]	♂	♂	♂	♂	♀	♀	♀	♀
Wing	272	256	254	262	260	259	252	257	278
Tail	163	172	172	177	186	184	180	195	172

[1] From Cory, Birds W. I., p. 185, 1889.

Lister says: "An inhabitant of the high woods It appears to breed during the months of April and May, though no one has yet been able to procure the young.

"The individuals that have been sent to Europe are birds that have been winged. During the latter part of August and the beginning of September I shot several examples that were moulting."

Ober says that it "is confined to the great central ridge running through the island. Like the Ramier (*Columba squamosa*) it feeds in the tops of the highest trees, its season for good condition being the later months of the year."

This fine bird is now decidedly rare on St. Vincent, where it is confined to the highest wooded slopes in the center of the island, behind Barrouallie. Some idea of its scarcity may be had from the fact that during a walk from Hermitage, in the upper Cumberland valley, south along the central ridge of the island only two were met with, although it is in this region that it is said to be most common. I stayed for four days in the Richmond valley, near the Morne Garou, where many parrots have previously been obtained, but neither saw nor heard one. Formerly it was very numerous, and was still common at the time of the great hurricane (1898). In that storm many were destroyed; two were picked up dead on the shores of St. Lucia, and a considerable number were disabled and caught by the natives. For days after the storm, parrots would be found in the smaller towns in a more or less helpless condition, due probably to hunger, for, as has been previously stated, the woods were at that time practically barren.

Before the species had recovered to any extent from the effects of the hurricane, the late eruptions occurred and probably killed many of the birds, as that part of the island best suited to them was laid waste.

In actions and general habits this parrot resembles *Amazona amazonica*. Like that species it is gregarious, and, in the days when it was abundant, occurred in large flocks. Now, however, it is only met with singly or in pairs. When flying it keeps up a loud and harsh "*kak-kak-kak*," the second syllable being louder than the first, and the third loudest of all. The flight is heavy and slow, like that of *A. amazonica*. When on the wing the bright orange speculum continuing into an elongated yellow patch on the primaries is very conspicuous. When in the trees these parrots keep

up a low and continuous jabbering, unless alarmed, when they become quiet. On being shot at they become extremely noisy and give out a series of shrieks and "*kaks*."

Owing to the steepness of the slopes and the nature of the undergrowth in the district where these birds occur, I found it exceedingly difficult to obtain specimens. Even if one were killed outright, a long search was necessary before it could be found, and to get wounded ones was usually out of the question.

When in the Richmond valley my native guide pointed out to me some very large dead trees, on a high ridge, where he said parrots used formerly to "camp" and about which they could be heard "barking" at any time. Probably these trees served as a nesting site for some of these parrots. None of the natives whom I questioned knew anything about the breeding habits of these birds, nor had it ever occurred to them that they might nest inside of trees, although many of them had found owls (*Strix nigrescens*) in such situations.

Mr. J. T. Thorne, until lately a magistrate in Demerara, who lived many years ago in St. Vincent, told me that a pair of these parrots once nested in an old estate chimney near Kingstown, and that two young were obtained from the nest.

?**Conurus** sp. Parrakeet. — Schomburgk ('**48**, p. 681) gives "*Psittacus passerinus*" as occurring in Barbados, and Hughes (**1750**, p. 73) says: "The Parakite. This is of the frugivorous kind, and about the bigness of a thrush, having a longer and more crooked bill. It feeds on all manner of berries, popaws, and ripe plantains, residing chiefly in inaccessible gullies. The bird borrows its name from its resemblance in make, but not in plumage, to the small green Parakite." Hughes was very accurate in his statements (*vide* under *Vireosylva calidris barbadense*), and is here confirmed by Schomburgk. From the writings of various early authors (Du Tertre, de Rochefort, Labat, etc.) we gather that parrakeets were formerly abundant on Martinique and Guadeloupe, and there is no reason why they might not have been plenty in Barbados also.

Owing to the flatness of Barbados and the consequent accessibility of all parts of the island, one would expect that any of the parrot tribe that existed there at the time of its discovery would very quickly disappear, inasmuch as they appear to be the most readily exterminated of all birds possessed of the power of flight.

Melopsittacus undulatus (Shaw). Warbling Grass Parrakeet. — While I was staying at the Marine hotel, Hastings, Barbados, in January, 1904, a bird of this species was to be seen every day flying about with a flock of blackbirds (*Holoquiscalus fortirostris*) which lived in that vicinity, as much at home as if they had been others of its own kind. This bird had been there several months. I was informed that it had escaped from a cage, and that a gentleman on the island had others which he intended to liberate in an attempt to introduce the species.

Ceryle alcyon (Linn.). Loggerhead Mango-bird; Kingfisher. — The Kingfisher is common from late summer till spring in all the islands, keeping near the sea. A few remain throughout the year.

Strix nigrescens (Lawr.). Jumbie-bird; Chawan; Owl. — Schomburgk gives *Strix flammea* as indigenous to Barbados. It is not at all improbable that this or a closely related subspecies was there in his day, although neither Hughes nor Ligon makes any mention of it.

This owl occurs rather sparingly all over St. Vincent, but is most common in the town of Kingstown, where it may be heard about the streets every night. There is a colony of them in the jail.

On the Grenadines it is only found on Bequia, but is rather common there, especially toward the northern end, and about the Spring estate. It has occurred on Union Island (where one was once captured in the church) and on Carriacou as an accidental visitor. It is common in Grenada, and may be seen every night flying about over the housetops in St. George's.

The nest is commonly placed inside of old houses, out-buildings, churches, hollow trees, etc. The eggs are three or four, white.

Chordeiles virginianus (Briss.). Nighthawk. — Col. Feilden has a male specimen of the Nighthawk which was obtained by Mr. Herbert Hart in St. Philip's parish, Barbados, on September 29, 1887. From what I learned while on Barbados, I consider Col. Feilden justified in believing this bird to be an annual visitor to the island. A bird answering to its description is well known to many of the people there, and I heard of several instances of its capture. The Nighthawk probably occurs casually in autumn and winter on all these islands.

Cypseloides niger (Gmel.). Black Swift. — Lister says

that this bird "may be seen flying over the pastures in great numbers after rain" in St. Vincent. The British museum collection contains specimens obtained in that island in May, 1890, by Mr. G. Whitfield Smith.

Chaetura acuta (Gmel.). Lesser Antillean Swift.— Lister says that this bird is the commoner of the two species of swifts on St. Vincent. There was a large colony of swifts in the chimney of the Montrose estate works near Kingstown which I presumed to be this species, although I did not obtain any specimens.

Chaetura cinereiventris guianensis Hartert. Guianan Swift.— Wells says that this bird occurs everywhere on Grenada, but is more numerous in the mountains. It does not occur north of that island.

Chaetura poliura (Temm.). South American Swift.— Common everywhere on St. Vincent and Grenada, especially in the woods and adjacent clearings. There are no swifts on the Grenadines.

Hemiprocne zonaris (Shaw). Ringed Gowrie.—Wells says: "On the 13th. July, 1882, I was travelling through Tuilleries estate (Grenada) and observed a large flock of birds hovering over a rocky hill. I got close up to them, and found them to be large swifts, with a white collar round the neck. I went back about a mile and borrowed a gun, but just as I got to the hill again, a hawk swooped down and dispersed them. I am told they frequent that particular hill every year. I saw several of them on the 9th. August about Grenville one afternoon after a heavy storm. I have no doubt they are identical with the 'Ringed Gowrie' described in Gosse's 'Birds of Jamaica.'"

Glaucis hirsuta (Gmel.). Brown Hummingbird.— This hummingbird is rather common in the more wooded portions of Grenada. It does not occur north of that island.

Eulampis jugularis (Linn.). Red-throated Hummingbird; Doctor-bird.— Ober says that at the time of his visit this hummingbird was the most numerous of all on the Soufrière. At the present time it is not at all common, and is almost wholly confined to the high woods.

I saw one on March 9, 1904, about a white cedar tree just behind the house of Rev. David Duffus in Bequia. Mrs. Duffus tells me that it is very rare on that island.

When alive this bird is readily distinguished by its large size, very dark color, and loud "*peep*," much like the cry of a lost chicken.

Sericotes holosericeus (Linn.). Green-throated Hummingbird; Large Doctor-bird. — I find I can match Gould's plates of *S. holosericeus* and *S. chlorolaemus* with specimens obtained on Barbados. The extent of the blue on the lower breast is a very variable character, and those birds in which it tends to shade into the green of the throat are apparently immature. Females usually, if not always, have longer bills than the males, and the blue on the breast is generally more restricted, tending to form a rhombic spot, and is not quite so sharply cut off from the green as in the males. I have examined a large series of this bird from all points in its range, and cannot see the slightest ground for subdividing it. The range of individual variation, as brought out by my series of twenty-eight examples from Barbados, is very great.

This hummingbird is common everywhere on Barbados. On St. Vincent and Grenada it is confined to the lower districts near the seacoast, and is not abundant, being, in fact, rather rare on the former island.

Among the Grenadines it is local. On Bequia I found it common in the town, and about the Spring estate. On Canouan only one was met with. At Union Island there were usually one or two to be found about some cedars behind the town of Ashton, and about another clump, midway between Ashton and Clifton. Two were seen on the flat land near Clifton Bay.

On Carriacou it was very common about the cedar trees near Hillsborough on the road to Harvey Vale, and was often seen at other points. I did not meet with it on the other keys. As a general rule in the Grenadines, wherever cedar trees are in blossom, one is apt to see this bird.

This is one of the few of the smaller West Indian birds I have seen at sea. I have met with it over the open water between certain of the Grenadines, and on September 23, 1904, while going from Montserrat to Antigua one of these birds appeared when we were about a third of the way across, and stayed about the boat for some time.

On August 27, 1903, I obtained at Barbados a female of this species with the throat white.

I have never seen but one nest of this bird. It was obtained at Belair, St. Vincent, and was composed of down, bits of fine leaves, etc., and was saddled on a small twig. There was one egg, white, the size of those of *Bellona cristata*.

Trochilus colubris Linn. Ruby-throated Hummingbird.— Col. Feilden says that this bird has been so accurately described to him that he has little doubt of its having occurred at Barbados. There are no records of actual capture for these islands, but it has been obtained on the Bahamas, Cuba, and Porto Rico.

Florisuga mellivora (Linn.). Jacobine.— On August 9, 1904, I procured an immature male of this species near the residence of Mr. G. Whitfield Smith, Top Hill, Carriacou. It was probably an accidental visitor, as I saw no others, and had it occurred on the island during the life of Mr. Wells, he would probably have noticed it.

There are many sloops trading between Carriacou and Trinidad, one of which this bird may have followed up from the latter island, where it is common. Mr. Chapman gives an interesting account of an example of *Volatinia jacarini splendens* coming up from Trinidad to Grenada on a steamer, and very likely this bird reached Carriacou by some such method. Possibly the northward extension of the range of certain South American birds (as *Molothrus atronitens*, *Sporophila gutteralis*, *Tyrannus melancholius satrapa*, and *Muscivora tyrannus*) in recent years may have been due in a measure to this habit.

Anthracothorax gramineus (Gmel.). Roscal.— A young male of this species was observed just behind the town of Ashton, Union Island, on September 9, 1904. It was the only example met with.

Bellona exilis ornata (Gould). St. Vincent Crested Hummingbird; Small Doctor-bird.— This bird is generally distributed over St. Vincent, but is not abundant at present. The nest and eggs resemble those of *B. cristata*.

Bellona cristata cristata (Linn.). Coulibre[1]; Small Doctor-bird.— The Coulibre is common on Grenada and on all the Grenadines. It is especially pugnacious and torments many of the larger birds, not even allowing other hummingbirds to feed on the same tree with it.

[1] According to Labat (**1722**, vol. 4, p. 317) this is the Carib name.

The nest is very small, constructed of fine dry leaves and cotton lint, lined with down. The eggs are two, white.

I have examined a specimen of this species (a male) with the crest perfectly white, taken on Grenada.

Bellona cristata emigrans Lawr. Barbados Crested Hummingbird; Small Doctor-bird. — This "Small Doctor-bird" is common all over Barbados, to which island it is confined. The nest and eggs resemble those of *B. c. cristata*.

Tyrannus dominicensis rostratus (Scl.). Rain-bird; Pippiree. — On Barbados this bird is an uncommon resident. I have seen it in St. Michael's (nesting), at Hastings near the Marine hotel, and obtained it in Foster Hall woods. On St. Vincent this is one of the commonest species, and it is abundant on all the Grenadines and on Grenada.

In actions it is much like *T. tyrannus*; its notes resemble "*pippiree pipipiree*" uttered sharply.

The nest resembles that of *T. tyrannus*, and is usually placed rather high. The eggs are three, buff, spotted with lilac and brown.

Tyrannus melancholius satrapa (Licht.). Yellow-breast Pippiree. — This bird occurs on Grenada, but is not common. On April 20. 1904, I took an adult female of this species at Clifton, Union Island.

Muscivora tyrannus (Linn.). Fork-tailed Flycatcher. — This is an annual visitor to Grenada and Carriacou, appearing in considerable numbers in August (according to Wells). I did not meet with it during my stay on Carriacou, but I found that the people were well acquainted with it. As a rule it frequents open ground. On Carriacou it is found about the low-lying pastures, particularly about Harvey Vale. On Grenada it is most common on the windward coast, about Grenville. It has never been known to nest in these islands.

On Trinidad and Tobago also this species is a migrant, coming over from the mainland during the wet season.

Myiarchus tyrannulus tyrannulus (Müll.). Loggerhead; Pippiree Gros Tête. — Mr. Riley (:**04a**, p. 275) has recently described a Myiarchus from St. Vincent and Grenada (the type locality being Grenada) under the name of *Myiarchus oberi nugator*. His series consisted of nine specimens: three from

Dominica, one from St. Lucia, two from St. Vincent, and three from Grenada.

I have reviewed the matter very carefully with a series of 68 skins from the West Indies: 4 from Dominica, 7 from St. Lucia, 17 from St. Vincent, 34 from the Grenadines (Bequia, Mustique, Mayreau, Union Island, the Tobago Keys, Prune Island, and Carriacou), and 6 from Grenada. These were compared with 21 specimens of true *M. t. tyrannulus* from Colombia, and three from Margarita Island, Venezuela, making in all 92 examples.

I have been unable to find any characters by which birds from Grenada, the Grenadines, or St. Vincent may be distinguished from continental specimens. There is no difference in size. The extent of the white markings on the wings is variable, for some birds from the Grenadines (agreeing with others from Colombia) have almost no white at all, while in others the bands are very wide. In the 57 birds from St. Vincent, the Grenadines, and Grenada, the rufous on the upper tail coverts is very conspicuous, more so than in the four from Dominica. In fact, in the living bird, as I am acquainted with it in these islands and on the mainland, it is a prominent characteristic. The colors of the head, back, and underparts are identical in birds in the same state of plumage from these islands and from Colombia.

The only character I have been able to discover by which specimens from the continent might be distinguished from others from Grenada, the Grenadines, or St. Vincent, is the extent of the brown markings on the tail. In examples from these islands the brown encroaches on the rufous of the inner web for an area just equal in extent to the outer web; that is, the brown area is the same on each side of the quill; on the outer it occupies the entire outer web, and on the inner a space just equal to it. As a general rule, the brown on the rectrices of continental specimens encroaches somewhat more on the rufous of the inner web; but this is not at all constant, one of the birds from Margarita Island having less brown than most of the Grenadine examples.

As in all other ways continental and insular (St. Vincent, the Grenadines, and Grenada) birds are identical, I am forced to consider them all as typical *M. t. tyrannulus*, and to treat the form as one which has worked its way up the islands from the continent as far as St. Vincent, in the same way that *Mimus gilvus*, *Molothrus*

atronitens, *Volatinia jacarini splendens*, *Merula gymnophthalma*, *Sporophila gutteralis*, *Elaenea martinica flavogastra*, *Tyrannus melancholius satrapa*, and a few others have done.

Mr. Cory ('92, p. 145) writes that his specimens of this bird from St. Vincent have light-colored bills, while those from the other islands are dark-billed. All the examples (17) which I procured on St. Vincent had dark bills; but I have seen old skins from that island (collected by Richardson) and others from St. Lucia (collected by Semper) in which the beak was light horn color. It appears to be due entirely to fading, as I never met with a bird in the flesh, nor handled a fresh skin with other than a dark-colored beak.

M. t. oberi from Dominica appears to be hardly worth more than subspecific rank. Newly moulted specimens of this form differ from newly moulted examples of *M. t. tyrannulus* in having only the wing bars dull grayish buff (instead of white) inclining to rufous, and having the brown on the tail occupying the entire outer half of the rectrices instead of only about the outer third, as in the case of the typical form.

The seven specimens from St. Lucia are intermediate between those from Dominica and those from the more southern islands.

Fading produces a great change in the colors of this bird. The feathers of the back on their first appearance are dark olive greenish, and the new feathers contrasting strongly with the worn ones, give the bird a spotted look. Dominica, in the localities inhabited by *M. t. oberi*, is very damp with a comparatively large rainfall, and the bleaching glare of the tropical sun is tempered by cloudy conditions, so that the birds retain their greenish cast until the beginning of a new moult. The color of the underparts also does not fade to an appreciable extent; but on the Grenadines, which are dry and hot, with practically no cover, the new feathers lose the greenish color and begin to turn brown even before the moult is complete. When the fresh plumage has been wholly assumed, therefore, the bird is of an olive brown color, quite different from fresh examples from Dominica, although the feathers on their first appearance were of exactly the same shade. As the fading increases the brown slowly becomes a brownish gray, and the underparts become lighter yellow. On Grenada, St. Vincent, and St. Lucia, the birds do not fade so much as on the more exposed Grenadines, but are nevertheless browner than those from Dominica.

This bird is rather uncommon on St. Vincent. It is found at the lower elevations, never in the high woods. The only locality where I found it in any numbers was at a place called Revelation, near Barrouallie. On the Grenadines it is usually common, frequenting scrubby growth, and it is common on all parts of Grenada.

The note of this species is a sharp "*whit*," uttered either singly or in a series. It is a rather stupid bird, and usually keeps near the ground. The food consists largely of berries which it obtains by hovering under them and reaching up.

The nest is constructed of sticks and leaves, and is placed in holes in trees or walls. It often contains a bit of snake-skin. The eggs are usually three, exactly like those of *M. crinitus*.

Blacicus flaviventris Lawr. — One specimen, the type, was obtained by Mr. J. G. Wells in St. Andrew's, Grenada, and another was seen by him on the Grand Etang road. This appears to be somewhat of a doubtful species.

Elaenea martinica flavogastra (Thunb.). YELLOW-BELLIED TOPKNOT.— This form is common on Grenada. On the Grenadines I obtained specimens on Bequia and on Mustique. On St. Vincent it is fairly common in the immediate vicinity of Kingstown, but I did not find it elsewhere.

It is rather remarkable that on the Grenadines and St. Vincent, both this form and *E. m. martinica* occur side by side. On St. Vincent *E. m. flavogastra* is only found in the Kingstown valley, and the other in the out-districts; but on Mustique I shot both from the same tree. Possibly *E. m. martinica* is the original inhabitant, and *E. m. flavogastra* a recent introduction from Grenada.

In life the three subspecies of *E. m. martinica* occurring in these islands are quite distinct. *E. m. barbadensis* has a cry sounding like the word "*peewhittler*," with a strong accent on the first syllable; *E. m. martinica* has the same note, but the accent is on the last syllable; *E. m. flavogastra* is intermediate. Moreover, *E. m. martinica* is usually seen singly, and frequents underbrush or low trees; *E. m. flavogastra* generally goes in small companies and is found in the upper parts of the trees, resembling *E. m. barbadensis* in this respect. All three are active birds, always on the alert, with crest erect. Their food is largely small berries, which they obtain in the same manner as does *Myiarchus tyrannulus*, by hovering under them and reaching up.

The nest of this bird is constructed of fine roots, grasses, bits of bark, and cotton lint, lined with feathers and cotton. It is very compactly made, and is usually placed flat on a large horizontal branch, or in the fork of two large branches. The eggs are two, delicate light pinkish buff, with large spots of lilac and brown at the larger end.

Elaenea martinica martinica (Linn.). Topknot. — On St. Vincent this bird is found on scrubby hillsides at low or moderate elevations. It is particularly common about Lowman's village, and from there up to the high woods. I did not meet with it at Chateaubelair, but obtained a number about Peter's Hope, where it occurred near the borders of the woodlands. In general habits this bird resembles *Myiarchus tyrannulus*, but is more active. One of its notes is a clear, long-drawn "*whe-e-ew*" with a falling inflection. It resembles a similar note of *E. m. flavogastra*, but can be distinguished on close acquaintance. Another call, often introduced by the one just mentioned, resembles the word "*peewhittler*" with the accent on the last syllable, repeated two or three times. The song resembles, as Wells says, the words: "*Ladies, ladies, ladies, you're lazy*" repeated over and over again. It has a peculiar tone, suggesting that of a wooden rattle. Every morning as soon as it begins to get light these birds begin their song, keeping it up almost without intermission until well after sunrise. I have never heard them sing at any other time. On the Grenadines the songs of this bird and of *Mimus gilvus*, which is most noisy at the same time, are the most characteristic of all the bird songs. In fact there are no other songsters there except *Merula gymnophthalma* which is an evening singer and not very common.

The nest and eggs are exactly like those of *E. m. flavogastra*.

Elaenea martinica barbadensis (Cory). Peewhittler.— Hughes (**1750**, p. 73) says, speaking of "The Pivet": "Altho' this bird feeds upon fruit, its bill is of the same make with those of the carnivorous kind; and it intirely subsists by berries or suchlike fruit of trees .... A Pivet is about the bigness and colour of our largest kind of sparrows [*Pyrrhulagra barbadensis*] and hath a wild chirping note."

Schomburgk ('**48**, p. 681) does not give this bird as a resident, although he mentions it as *Elania pagana*.

The Peewhittler is common on Barbados wherever there are

patches of woodland or groves of trees. Like the two other subspecies, it is largely frugivorous.

The nest and eggs resemble those of *E. m. flavogastra.*

Estrelda astrild (Linn.). Pink-bellied Waxbill.— A male example of this bird in unworn plumage was obtained on August 17, 1903, on the Foster Hall estate, St. Joseph's, Barbados. It was feeding in company with a common Grass-bird (*Tiaris bicolor omissa*). Although probably an escaped cage bird, still this species may have obtained a footing on Barbados, as it has been a favorite bird for introduction into new localities, and appears to be well established in a number of places, among others Madagascar, Mauritius, and St. Helena.

Dolichonyx oryzivorus (Linn.). Bobolink.— The Bobolink is an annual, though rather uncommon visitor to these islands. A number of specimens have been obtained on Barbados by Mr. Herbert Hart, Dr. C. J. Manning, Col. Feilden, Mr. W. Lambert Philips, and others. Mr. Wells once killed two out of a flock of five on the eastern side of Grenada.

Molothrus atronitens (Cab.). Cowbird.— Wells writes that this bird was not observed in Carriacou until June, 1899, when flocks of from six to ten were to be seen about Hermitage, and Harvey Vale pasture. It is now common on Carriacou, especially about Beausejour and Harvey Vale, and has spread to the neighboring islands, being found on Union Island about the savanna where the stock are pastured and about Bloody Bay on the northern coast, on Petit Martinique, Mayreau, the Tobago Keys, and Canouan.

On Grenada it has become well established, occurring generally over the island, and commonly in the Botanic gardens, about Grand Anse, and the Woodlands estate. Mr. W. E. Broadway, the curator of the Botanic gardens tells me that he first noticed the bird at Ballast Ground about four years ago. I saw a number of specimens of this bird in the collection of Mr. Charles Vernet at St. George's, who told me he had only met with it within the last two or three years.

In habits this bird closely resembles the common Cowbird (*M. ater*). Its song is rather pleasing, but weak. It is very much like that of *Euphonia flavifrons.*

I saw some eggs in the collection of Mr. J. G. Wells at Carriacou which were supposed to be of this bird. They were dull green with

rounded spots of black (like those on the eggs of *Ampelis cedrorum*). It is said by the natives to be non-parasitic.

Xanthocephalus xanthocephalus (Bonap.). YELLOW-HEADED BLACKBIRD. — Col. Feilden says: "Dr. Manning procured a specimen of this species in the autumn of 1887, which he kindly placed in my collection." The only other West Indian record is from Cuba, where Dr. Gundlach once purchased one in the market at Havana.

Holoquiscalus fortirostris (Lawr.). BLACKBIRD (Barbados). — Hughes writes: "These birds are very numerous in this island (though there are none at Antigua) . . . . They are serviceable in destroying crickets and other vermin; yet this scarce compensates for the ravage they make in consuming our Indian and Guiney corn, the former chiefly when young; the latter, some after it is planted, as well as when ripe."

Ligon says: "The next is a Blackbird, with white eyes, and that so ill become her, as she is accounted an unhandsome bird; her voice is harsh, somewhat like our jay in England; they go in flocks and are harmful birds, for they are great devourers of corn and blossoms of trees, and the planters wish them destroyed, though they do not know which way. They are a kind of Stares [Starling], for they walk and do not hop as other birds. One thing I notice in these birds, which I never saw in any but them, and that is when they fly, they put their train into several postures; one while they keep it straight as in other birds; sometimes they turn it edgeways, as the tail of a fish, and by and by put it three square with the covering feathers atop, and the sides downwards."

This bird is common all over Barbados, especially about the estate works. Albinism appears to be rather common in this species. In September, 1903, I shot a male with some white feathers in its head at Grazettes, St. Michael; and while staying at the Marine hotel at Hastings during the first two weeks in January, 1904, I saw two partial albinos in a flock which lived in a large tree just outside my window. I had a good chance to observe them, as they used to come, in company with many others, to the gallery just under my window every morning to be fed. One had the third left primary white. This bird also had a deformed bill; the upper mandible was much arched, giving it something the appearance of an Ani. The other had several white feathers in each

wing; both were males. Dr. Manning tells me that he has taken two pure white examples at Black Rock.

These, like the others of the genus, are bright, active birds, with a great variety of notes. They are very noisy, keeping up an incessant jabbering when in a tree. Sometimes they will all suddenly become quiet, then give out a number of notes like "*chee, chee,*" sounding then like a flock of Redwings (*Agelaius phoeniceus*). This only lasts a minute or so, then the jabbering begins again. The latter is a characteristic mixture of varied notes, and, if not sweet, certainly is not unpleasant.

This bird has a number of peculiar postures. One will be walking about, and suddenly stop, smooth down its feathers, point its bill straight up in the air, and hold this position a minute or so. Often two do this together, facing each other.

The song is a series of four whistling notes, the first and third strongly accented, and the last weak and prolonged. The local rendering of the song is: "*We sha'n't be long.*" In singing, the bird ruffles up all its feathers, throws back its head, spreads its tail, and slightly spreads its wings. In flying, as Ligon noticed, the tail appears to be held in all sorts of ways; but on alighting it is usually brought down, spread out, and keeled, acting as a brake. About houses this bird is very tame, but in the country it is shy.

The nest is large and coarse, and there are usually several in the same tree. As a rule it is placed from six to fifteen feet from the ground. The eggs are generally three, light green, with black and dark brown spots, blotches, and scrawls, like those on the eggs of the Redwing (*Agelaius phoeniceus*).

Schomburgk says that this species is "said to have been introduced into Demerara, where they are now numerous. As a counter-present, Barbados received its crapaux [*Bufo agua*] from that colony." It has also been introduced into St. Croix, St. Kitts, and Antigua.

Holoquiscalus dispar Clark.

BEQUIA SWEET; "BARBADOS" BLACKBIRD.

Holoquiscalus dispar Clark, Proc. biol. soc. Washington, vol. 18, p. 61, Feb. 21, 1905.

So rare are specimens of this bird in collections that Mr. Ridgway was unable to examine one at the time he wrote his account of the genus Holoquiscalus for Part 2 of his "Birds of North and Middle America," and was forced to refer it questionably to *H. inflexirostris* of St. Lucia. Mr. Cory also, at the time he wrote the "Catalogue of West Indian birds" had but a single specimen, a male, and also referred it to *H. inflexirostris*. As a matter of fact, *H. dispar* is quite different from that species, and from *H. luminosus* of Grenada, the female being dull black, even darker than the female of *H. fortirostris*. The bill of *H. dispar* being much the same as that of *H. inflexirostris* does away with the chance that the bird might be the *Quiscalus mexicanus* of Cassin, as Cassin's type was a stout-billed bird like *H. martinicensis*.

This species is confined to St. Vincent, and is only found in the Kingstown valley and the neighboring windward district, where it is not very common. There is a small roost of them on the side of Dorsetshire Hill, just behind the town. It is called the "Bequia Sweet" by the peasantry from its notes, which resemble the syllables "*beck-way*[1] *sweet*," and from its resemblance to *H. luminosus*, which is abundant on that island. The name "Barbados Blackbird" is given to distinguish it from the common "Blackbird" (*Coereba atrata*), and, of course, from its resemblance to *H. fortirostris*. In habits this species resembles *H. luminosus*.

The nest and eggs are like those of *H. fortirostris*.

Holoquiscalus luminosus (Lawr.). MERLE; BLACKBIRD (Grenada).— This bird is common on Grenada and abundant on all the Grenadines, flying about from one to another. In actions it resembles *H. fortirostris*, but its notes are slightly different. The usual cry resembles, as Wells suggests, "*green corn sweet.*" It does great damage by digging up newly planted Indian corn, and

[1] "Beck-way": the local pronounciation of Bequia.

by tearing to pieces the young ears. At night it usually roosts in great flocks. All the birds in a certain district spend the night in one tree, and generally choose one that is large, more or less isolated, and conspicuous. On Carriacou there is a good-sized roost near Beausejour estate, another near Mount d'Or, and several more in different parts of the island. The largest in the Grenadines is in the middle of the town of Ashton, Union Island. There is a tall tree here which harbors many hundreds, and all the lower trees behind the town hold them by scores. They begin to collect an hour or so before dark, arriving in small or medium-sized companies. On Easter Sunday, 1904, there was an unusually heavy rain which killed a large number of these birds. The ground under the main roosting tree was strewn with their dead bodies.

The nest and eggs resemble those of *H. fortirostris*.

Pyrrhulagra noctis crissalis Ridgw. Robin; Sparrow.— This bird is fairly common on St. Vincent about the towns, but is rarely seen far from houses, and never in the woods. It frequents especially the large-leaved breadfruit trees (*Artocarpus incisa*), and is often to be found about the arrowroot works, feeding on the arrowroot. The notes of this bird are clear and loud, sounding like "*whéou, whéou, whéou.*" It also has a characteristic chirp.

The nest is a bulky domed affair with the entrance on one side. The eggs are white, evenly and finely speckled with lilac and red brown.

Pyrrhulagra noctis grenadensis Cory. Red-throat See-see.— This subspecies is abundant all over Grenada. In habits it is just like the preceding form, and the nest and eggs are the same.

Pyrrhulagra barbadensis (Cory). Sparrow.— This bird is very common on Barbados, and, about the houses, very tame, entering them freely. The Rev. Canon Bindley writes: "I have had a sparrow perch atop of a book as I held it in my hand reading; who, after liberally helping himself to toast and bananas, appeared to desire now to gratify an intellectual appetite hitherto unsuspected. One morning the same greedy creature actually fell into the milk jug, having overbalanced himself in his endeavors to reach the milk, and was rescued half drowned. Taking a half circle flight outside, he re-entered the window and, with feathers still milky, began another raid on the buttered toast. Sometimes, however, this excessive domesticity is destruction of more valuable

things than small eatables. I remember when a large table had just been set for dinner seeing a sparrow fly into the room and alight upon the edge of a champagne glass. This he at once upset by his weight, and it fell to the floor with a crash. He then coolly hopped to the next glass with the same result, and probably would have gone the round of the table had he not been at once detected and banished from the room. Worse still, a sparrow has been known actually to ruin a wedding-cake during the absence of the bride at church, chipping the icing with his beak, and rolling the sugar presentment of Cupid on the floor."

Tiaris bicolor omissa (Jard.). Grass-bird; Cane Sparrow. — In the rather large series of this bird which I obtained from these islands, I am unable to find any characters by which specimens from any one island may be differentiated. Those from Barbados and Grenada agree with others from the Grenadines and St. Vincent. The extent of the black on the underparts and on the head is exceedingly variable. One or two of the females show traces of black on the chin and upper throat. A male obtained by myself on Margarita Island can be exactly matched by others from these islands.

The Grass-bird is abundant in all these islands, with the exception of some of the smaller Grenadines (notably Prune). It is the commonest bird on Barbados and Grenada, but on St. Vincent *Coereba atrata*, and on the Grenadines *Mimus gilvus* are perhaps more abundant. On St. Vincent and Grenada it is not found in the high woods.

This little bird is found mainly in open places, especially in grassy pastures. It keeps near the ground, in the grass or in low bushes. The song is a weak buzzing trill, like that of *Coereba atrata* or *C. wellsi*, and is given with the wings slightly elevated and the head thrown back.

The nest is a rather bulky domed structure, entered from the side, and is usually placed rather low. The eggs are three, sometimes four in number, white, spotted, especially about the larger end, with reddish brown. They resemble the eggs of *Coereba wellsi* somewhat, but the ground color is usually a clearer white, the spottings more distinct, more reddish, and more segregated about the larger end.

Sporophila gutteralis (Licht.). White-beaked Grass-bird.

— This bird is common on Grenada, especially about St. Patrick's. I found it not uncommon on Carriacou, along the central ridge of the island, from Belair to Chapeau Carré. As Mr. Wells did not report it from there, it is probably a recent arrival, but appears to be well established. On September 15, 1904, I heard, and subsequently saw an example of this species in the grounds of the Agricultural school, at Kingstown, St. Vincent.

It has a very loud voice for such a small bird. The song is clear and sweet, suggesting that of the Indigo-bird (*Cyanospiza cyanea*), and is usually given from a considerable elevation; in fact, this species is oftener seen in the tree-tops than near the ground, although it feeds largely on the seeds of grasses. It is very shy for such a small bird.

Volatinia jacarini splendens (Vieill.). Glossy Grass-bird. — Wells says: "Rather shy (on Grenada): frequents pastures and guinea-grass fields, on the seeds of which it feeds, running along under the grass and picking up the seeds. Is fond of perching on a small dry shrub and springing up into the air several times, uttering a prolonged '*chur-r*' always alighting in the same spot again. "Nest, in tuft of grass. Eggs white, thick brown spots at large end, and scattered smaller ones of same color on rest of egg."

I only saw two or three examples of this bird, in St. Andrew's, Grenada. It appears to be rather local.

Mr. Chapman says: "While *en route* from Trinidad to Grenada, a female of this species boarded the steamer. We were then about half way between the islands. The bird was in an exhausted condition, and was caught without difficulty. We anchored about half a mile off the harbor of St. George's, Grenada, where I have no doubt the bird went ashore, as I did not see it after leaving the island." This is interesting in showing how certain species may have been brought first to these islands and assisted in becoming established.

Paroaria cucullata (Lath.). Brazilian Cardinal. — On January 10, 1904, at Hastings, Barbados, I saw a single example of this species. It was probably an escaped cage bird.

Sicalis arvensis luteiventris (Meyen.). Grass Canary. — Very common in St. Philip's parish, especially near the Crane hotel. Mr. A. A. Evelyn of Spencer's (Christ Church) writes that it may be seen in flocks of fifty to a hundred in his district. It has been recently introduced into Barbados.

Euphonia flavifrons viscivora Clark.

MISTLETOE-BIRD; BLUE-HEAD; LOUIS D'OR.

Euphonia flavifrons viscivora Clark, Proc. biol. soc. Washington, vol. 18, p. 19, Feb. 2, 1905.

This bird is common on St. Vincent on the higher and steeper slopes, especially in the upper Cumberland valley, and in the woods behind Mt. Wynne and Peter's Hope estates. I saw two in the woods behind Chateaubelair, and found it fairly numerous in winter in the Clare valley, and on Fort Charlotte Hill.

This species would often pass unnoticed were it not for its loud voice, as it usually keeps well in the inner part of the trees and bushes, and is just about the size of the leaves of the trees upon which it is most often seen. Although common, it is rather difficult to procure owing to the precipitous nature of the slopes it inhabits, unless one is fortunate enough to discover a loblolly tree with fruit, or a silk-cotton tree just budding, where, if there are any about, they will be found in abundance.

The call notes of this bird are three in number. One is a plaintive whistle, somewhat like the whistle of the Redwing (*Agelaius phoeniceus*), another is a chatter like that of the Baltimore Oriole (*Icterus galbula*), but lower pitched and not quite so loud, and the third is a characteristic quick and sharp double chirp. The last is the usual alarm note, but may be given at any time. All the notes are clear, and loud for such a small bird, and can be heard a long way across the valleys on a still day. The song is low and sweet, occasionally punctuated by a clear whistle. Except for the whistling note, it bears a strong resemblance to that of *Molothrus atronitens*. In singing, a position is generally chosen in the lower branches of a tree, near the trunk, and the bird is at such times very unsuspicious. It is usually met with in little parties of from six to a dozen.

On Grenada it is not very common, and is only found in the higher parts of the island.

Calospiza versicolor (Lawr.). GOLDEN TANAGER. — This bird is not very common on St. Vincent. It is found in the higher parts of the island, but is sometimes seen in the lowlands, particu-

larly about Edinboro' and Lowman's Village. At Chateaubelair I only met with four or five during my stay of about a month.

The song of this species, which is much like that of the St. Vincent Wren (*Troglodytes musicus*), is a series of half a dozen loud and clear whistling notes, increasing in volume, and ending abruptly. It is introduced by a squeaky sound that suggests the song of the Palm Tanager (*Tanagra palmarum*).

When high up in the trees this species usually appears of a red gold or burnished copper color, the wings and tail appearing black; but when in the low bushes it may appear straw yellow, bronzy, or bright green, according to its position with reference to the light.

This species is confined to the island of St. Vincent.

Calospiza cucullata (Swains.). Sour-sop Bird; Bluebird. — This species is confined to the island of Grenada, where it is everywhere common. It usually keeps rather low, in small trees or bushes, but is often seen high up in the trees. In actions it resembles *C. versicolor*, but the song is different — much like that of *Tanagra palmarum*, but considerably less squeaky and disagreeable. It has a very characteristic chirp.

The nest is very like that of the Purple Finch (*Carpodacus purpureus*) but not quite so compact. It is usually placed about six feet from the ground, but may be much higher. There is a great deal of variation in the color of the eggs, some being white thickly covered with longitudinally elongate streakings and spottings of gray (in some fairly uniform, in others mainly confined to a ring about the larger end); and others white, with gray and brown markings, or with spots of various shades. The nesting season is early spring.

Piranga erythromelas Vieill. Scarlet Tanager. — There is a specimen of this bird in the United States national museum labeled as having been obtained in Barbados.

Progne dominicensis (Gmel.). West Indian Martin. — Schomburgk gives this bird as a visitor to Barbados in his time. It has not been found there in recent years.

On St. Vincent it is common about the sea cliffs near Barrouallie, and is often seen flying about at other points, especially on the devastated district at the base of the Soufrière, about the Kingstown valley, and in the windward district.

On the Grenadines it breeds in the church at Canouan, and at

various places on Carriacou. I have seen it on Mayreau and Petit Martinique, and stray examples at Ashton and Battery Hill, Union Island.

It is common on the lowlands of Grenada.

Hirundo erythrogastra (Bodd.). Barn Swallow.— Hughes (1750, p. 73), says: "As the make of this bird every way answers the description of those of the same species [*H. rustica*] in England it would be needless to describe it." He says further that in the winter (?) months "they retire to their holes in the rocks, and do not appear during those months."

The Barn Swallow is common in all these islands from August until March, appearing in large flocks at Barbados and Carriacou. I have seen it on St. Vincent, and on Mustique, Bequia, and Union Island among the Grenadines.

Vireosylva calidris barbadense Ridgw. Monkey-bird; Lady-bird; Ladies' Related.— A comparison of the measurements of 23 males and 19 females of this form from St. Eustatius to Grenada, including 6 breeding birds from Barbados and 7 from the Grenadines (Bequia, Union Island, Prune, and Carriacou), shows that, while the individual variation is rather large (largest male, wing, 82, tail, 66, culmen, 15, tarsus, 20, Barbados; smallest male, wing, 75, tail, 57, culmen, 16, tarsus, 20, Grenada; largest female wing, 79, tail, 65, culmen, 15, tarsus, 20, Dominica; smallest female, wing, 75, tail, 56, culmen, 16, tarsus, 19, Grenada) it would be impossible to divide this form further on the basis of measurements alone. I have a male from Carriacou larger than that given by Mr. Ridgway (Birds No. and Middle Amer., pt. 3, p. 140, 1904) from St. Lucia. My four St. Vincent birds are much larger than the three recorded by him, while all the measurements he gives may be duplicated in my series of Grenadine examples alone.

The color of this bird is exceedingly variable; but my series shows that it is wholly dependent on the season at which the birds are taken. When perfectly fresh, the bird is bright olive green above, with sides of the head light gray, the pileum brownish gray, this color distinct from the olive of the back and not grading into it, as in *V. c. calidris*, and the under parts white, with the sides, flanks, and under tail coverts tinged with sulphur yellow. The feet are slaty-blue, and the iris is reddish brown. Mr. Nicoll's (:04, p. 563) description and plate of "*Vireo laurae*" refer to a bird of this sub-

species in a fresh condition. He says (*loc. cit.*) that *V. laurae* is "somewhat similar to *Vireo calidris*, but is much smaller, and of more intense coloration." I have birds even smaller and brighter than that figured as the type of *V. laurae* from the Grenadines and St. Vincent. Lawrence's description of *V. calidris* var. *dominicana* (Proc. U. S. nat. mus., vol. 1, p. 55, 1878) is essentially the same as Nicoll's of *V. laurae.*

After the assumption of the new plumage, the bird begins to get lighter and more grayish, and quickly loses the intense olive of the back, which becomes olive gray, while the cap loses its bluish cast, and tends to approach the grayish color of the back. The birds inhabiting the higher and more shaded districts (on Dominica, St. Lucia, St. Vincent, Grenada, etc.) never get beyond this stage; but on the more open areas (such as Barbados, the Grenadines, and the lowlands of St. Vincent and Grenada), they begin to assume a brownish color, which may go so far as to leave the bird a uniform dingy brownish gray above (head and back), with almost no yellow beneath, entirely different from the colors of fresh specimens. The type of *V. c. barbadense* (*vide* Ridgway, *loc. cit*), as well as five examples collected by myself on that island, and a number of others from the Grenadines are in this condition. This fading begins immediately after the moult is complete, and progresses very rapidly on Barbados and the Grenadines, less so on the lowlands of Grenada and St. Vincent, while on the higher levels of these last-named islands it is sometimes scarcely perceptible. Fresh specimens from the islands southward of Guadeloupe are identical in color; but two birds from Marie Galante show a tendency to approach *V. c. calidris* in having the color of the cap shade into the green of the back.

Hughes, writing in 1750 (**1750**, p. 73, "The Spanish Lacker") said: "This bird is most commonly to be seen near Hackleton's Clift." At the present day it appears to be a breeding resident in this region only, although specimens are occasionally taken at other parts of Barbados. It is not a very common bird, but I found a considerable colony of them in Foster Hall woods, where I also found the empty nests and saw the young following the parents. Were it not for its loud notes the bird would often escape notice. It is interesting to note that Schomburgk ('**48**, p. 681, "*Vireo olivacea*") gives this species the local name of Monkey-bird by

which name it is known to-day among the peasantry of Barbados. Col. Feilden considers this bird an autumnal and winter visitor only; but his notes appear to have been made in the southern part of the island. It is possible, as Mr. Cory suggests, that the birds about Hackleton's Cliff and in Foster Hall woods are permanent residents, and the others, picked up from time to time at other parts of the island, are visitors.

This species is fairly common on Grenada, less so on St. Vincent, but more so on the Grenadines. It is found in all situations, except perhaps the highest and deepest woods, but is most common on the borders of woodland and about the edges of mangrove swamps. In habits it resembles *V. olivaceus*, and the nest and eggs are similar.

Coereba barbadensis (Baird). YELLOW-BREAST; SUGAR-BIRD. — Like all the Honey Creepers (Coereba) this is a very active little bird, rarely still a minute. It occurs commonly all over the island of Barbados, in the woods as well as in the open pastures, among the topmost branches of tall trees, and near the ground in small bushes. Its chirp resembles that of the local "Swamp Sparrow" (*Dendroica striata*). In general its actions resemble those of the Goldfinch (*Carduelis carduelis*) and it has much the same manner of flight. Wounded birds of this species are very quick to take cover under stones, logs, or leaves.

Coereba atrata (Lawr.). MOLASSES-BIRD; YELLOW-BREAST; SUCRIER.— 1. Normal form *saccharina* (Lawr.). — This bird is at present exceedingly rare, if not actually extinct. Ober succeeded in obtaining two specimens, but I failed to find any trace of it whatever. The fact of its having local names (Molasses-bird; Sucrier) would seem to suggest that it was formerly common on St. Vincent. Lister makes no mention of it.

2. Melanistic form *atrata* Lawr. BLACKBIRD. — This is one of the commonest birds on St. Vincent, and is found everywhere, except in the high woods. Its favorite haunts are banana patches and cocoa groves. The notes resemble those of *Tiaris bicolor omissa*, but are a little clearer, and it has also a characteristic chirp.

The nest is constructed mainly of grasses, and is domed, with the entrance on one side. The eggs are three, white, thickly spotted with light brown, some uniformly, others more heavily marked about the larger end.

Coereba wellsi (Cory). SUCRIER; YELLOW SEE-SEE. — 1.

Normal form *morrisi* Clark.— This bird is very rare on Grenada. Ober says that it "is not found in great numbers, as in some of the northern islands [? Grenadines]; indeed I have seen it but twice — on the mangrove flats of Point Saline." This is inserted under the heading "*C. atrata*," but must refer to the Grenada Yellow-breast, as no black species occurs on any of the "northern islands" (either Grenadines or northern Lesser Antilles), and the black form of this bird is abundant all over Grenada.

While I was staying at St. George's, Grenada, Mr. Charles Vernet very kindly presented me with a specimen of this form which he had taken himself in the vicinity of Point Saline. He told me it was the only one he had ever seen. The bird is indistinguishable from Grenadine examples, and, except in color, from a series of the black form from Grenada.

On the Grenadines, this bird is abundant, and is the most characteristic feature of the avifauna. In habits it exactly resembles the black variety of Grenada.

The nest and eggs are like those of *C. atrata* of St. Vincent, but the eggs are slightly smaller. The nests are sometimes placed in queer situations; there is one in the chandelier of the church at Hillsborough, Carriacou, and Mr. Wells saw one which was built in a tethering chain hung up for sale in a shop in the same town. The usual situation is a low bush, but I have seen one constructed at least twenty feet from the ground in a large tree. In the vicinity of cotton fields, the cotton lint is largely used in the building of the nests.

2. Melanistic form *wellsi* Cory. Black See-see.— This form is abundant all over Grenada, except in the high woods. It is confined to that island and is never found in the Grenadines.

The nest and eggs are identical with those of the preceding form.

Coereba luteola (Cab.). South American Honey-creeper. — This bird is accidental on Grenada. A specimen was obtained about the year 1886, and described by Mr. Cory ('89, p. 219) as *Certhiola godmani*.

Compsothlypis americana (Linn.). Parula Warbler.— Col. Feilden writes that Mr. Herbert Hart of Fairfield, St. Philip's, Barbados, gave him a mounted specimen of the Parula Warbler which he had shot in his garden in the month of June. He himself recognized one in a garden at Hastings on November 4, 1888, and subsequently met with others in different parts of the island.

There are no records for St. Vincent or for Grenada, but it is probably an annual visitor in small numbers, as it has been recorded from practically all of the other Lesser Antilles.

Dendroica striata (Forster). SWAMP SPARROW; BLACK-POLL WARBLER.— One example was obtained by Col. Feilden on October 20, 1888. He saw others, however, and considers it a regular winter visitor to Barbados. It has never been taken on St. Vincent or on Grenada.

Dendroica ruficapilla (Gmel.). YELLOW-BIRD.— The subspecies of this form, *D. r. ruficapilla* (Guadeloupe and Dominica), *D. r. rufivertex* (Cozumel Island), *D. r. flavida* (St. Andrew's) and *D. r. rufopileata* (Curaçao), appear all to fall within the range of individual variation, if we can judge from the great differences exhibited by a series of sixteen specimens of the closely related *D. capitalis* of Barbados. The only specimen from Cozumel Island which I have been able to examine, as well as three specimens from Dominica (two kindly loaned by Dr. Louis B. Bishop) are inseparable from Grenadine examples.

This bird is rare on Grenada and rather shy, frequenting the mangroves about the swamps on the windward side of the island. At Carriacou it occurs rarely in the swamps at Harvey Vale. On Prune Island it is abundant in a swamp near the northern shore, and is common at other points on the leeward coast. On Union Island it is found in an extensive mangrove swamp near Ashton, and I have heard it in a swamp near Bloody Bay in the northern part of the island.

In habits it resembles *D. aestiva*, but its song is less varied. It is almost never seen outside of the mangrove swamps.

NOTE.— Mr. Ridgway gives (Birds No. and Middle Amer., vol. 2, p. 510, 1902) *Dendroica aestiva* as being unquestionably recorded from Grenada. I have examined the specimen upon which he based the statement, and find it absolutely indistinguishable both from *D. aestiva* and from *D. ruficapilla* in the same state of plumage. It is an immature male. As Mr. Ridgway at the time he wrote, was unaware of the occurrence of a resident Yellow Warbler on Grenada, and there is no way of telling which the bird really is, I have thought it best to regard it as an example of the local resident form.

Dendroica capitalis (Lawr.). YELLOW-BIRD; YELLOW-HAMMER.— This bird is common on Barbados, especially about pastures

in which grow clumps of seaside grapes (*Coccoloba uvifera*). In habits and song it closely resembles *D. aestiva*.

Catharopeza bishopi (Lawr.). Black and White Soufrière-bird.— Although I spent a long time in different parts of the high woods of St. Vincent hunting for this bird, as I was particularly anxious to obtain a good series, I neither saw nor heard one. If it exists at all at the present time it is exceedingly rare. It is wholly unknown to the people on the island.

Ober, who discovered this bird, says that "it is very rare and very shy, and is found in the crater and dark gorges of the Soufrière." He writes further: "Its note is very sharp; either the male or the female give utterance to the syllable '*few few few*' etc., eight or ten times, immediately answered by the mate with '*whit whit whit*' etc., the same number of times."

Lister says: "This little bird is entirely confined to the high woods. In the stomach of one I found a small newt. This species may often be observed searching about amongst the stones and decayed logs that strew the courses of the mountain streams. The iris is hazel."

Seiurus noveboracensis (Gmel.). Water-Thrush. — Col. Feilden noted an example of this species at Brandon (Barbados) the residence of Mr. Edmund Taylor, on November 5, 1888, and another, which he secured, at Chancery Lane on the 24th of the same month. It is probably of regular occurrence in the autumn and winter, but is frequently overlooked because of its retiring habits and somber colors.

Mr. Wells has observed it on Carriacou all the year round. It occurs regularly on St. Vincent, the Grenadines, and Grenada, wherever there are mangrove swamps. It is comparatively seldom seen, being surprisingly shy for such a small bird, but its loud and characteristic note is often heard in the swamps.

Setophaga ruticilla (Linn.). Goldfinch; Christmas-bird; Redstart.— This bird is common on Barbados, St. Vincent, and Grenada, arriving in the middle of September and remaining until February. On Barbados it is most common in the Scotland district, and about Foster Hall and Joe's River woods. On St. Vincent and Grenada it is found on moderate elevations, but not in the high woods. There are no records for the Grenadines; possibly these islands are too open and too dry to offer it any attractions.

Troglodytes musicus (Lawr.). Wall-bird; St. Vincent Wren.— Ober records this bird as common at the time of his visit. It appears to be rare at present; I only met with it three times: once on the border of the high woods behind Peter's Hope, once in Revelation valley, and once (heard singing) in the Botanic gardens, Kingstown.

The song is loud and clear, of five or six whistling notes. It also has a peculiar mellow chatter, something like that of *Euphonia flavifrons* but louder.

The nest, I was told, is constructed in holes in old walls or trees. I examined one in a large cabbage palm on Fort Charlotte Hill where the people said the birds had bred in former years.

Troglodytes grenadensis (Lawr.). God-bird; Grenada Wren.— This species is common all over Grenada. In habits it resembles others of the genus. The song is like that of *T. musicus* of St. Vincent.

The nest is constructed in holes and recesses, of fine dry roots, etc., lined with feathers. The eggs are four, sometimes five, dirty white, thickly sprinkled with light reddish brown specks, and resemble those of *T. aedon*.

Cinchlerminia sanctae-luciae (Scl.). St. Lucia Mountain Thrush.— Ober writes: "Have heard the unmistakable whistle of this bird [*C. dominicensis*, which he observed on Dominica] and have seen it as it flitted by in the dusk of the high woods, but have not obtained it." I found no trace of it on St. Vincent, nor were any of the natives acquainted with it.

Merula gymnophthalma (Cab.). Yam-bird; Yellow-eyed Grieve.— On St. Vincent this bird is confined to the immediate vicinity of Kingstown and about Edinboro', where it is fairly common, especially in the Botanic gardens.

On the Grenadines it occurs on the northern end of Bequia, on Canouan, on Union Island (about Clifton), on Petit Martinique, along the high central ridge of Carriacou and in the lowlands at its southern end, and on Isle Ronde, but is nowhere common on these islands. It is common all over Grenada.

In habits the Yellow-eyed Grieve resembles the American Robin (*Merula migratoria*), but is much more shy and secretive. It is usually to be found in the interior of trees having thick, dark foliage, such as the mango (*Mangifera indica*), but sometimes,

especially in the Grenadines, is met with in scrubby growth. Occasionally it is seen on the ground hunting for insects after the manner of the Robin, but is at such times very suspicious. The alarm note is a melodious "*chut*," with a characteristic intonation. The usual call note is a liquid "*pe-ou'-wou*," entirely different from the call of any other bird with which I am acquainted, but suggesting the squeal of the Ani. The song, which is usually heard in the evening just before sunset (rarely in the early morning), is very like that of the Robin, but lacks the peculiar high and strained notes occasionally given by that species, being continuous, with little variation in the quality of the notes.

In life the bare skin about the eye is very conspicuous; it is bright yellow, inclining to orange, becoming orange on the eyelids. It is the same in both sexes. The bill is greenish yellow becoming brown at the tip; the feet are light slaty, and the iris is brown.

The nest is like that of the Robin, and is usually placed rather low, a favorite situation being in a cocoa tree. The eggs are dull green, rather thickly speckled with reddish brown, especially toward the larger end. They are very variable; in some, the spots are very large, in others minute; in some evenly distributed, in others confined to a ring about the large end.

This species was introduced into Barbados from Grenada in 1902, and in the next year a pair successfully raised a brood in the vicinity of the Garrison at Hastings.

Merula nigrirostris (Lawr.). Grieve; Mountain Grieve.—On St. Vincent this bird is not rare; it is found in the woods, about the clearings and in the vicinity of the mountain streams, most commonly in the upper part of the valleys behind Barrouallie and Chateaubelair. It is common in the Botanic gardens at Kingstown, where it is found with *M. gymnophthalma*.

It does not occur on the Grenadines, but is found in the deep woods on Grenada, where it frequents the valleys along the mountain streams.

In actions it resembles *M. gymnophthalma*, but is much less commonly seen in the open, and more often in the upper parts of trees. It has the same nervous flitting of the wings and tail observable in that species and in *M. migratoria*.

The alarm note is something like that of the Robin, but lower, and not so loud. Its call is a peculiar cry, unlike that of any other

thrush that I know. The cry of the young of both this and the preceding is like that of the young of the Robin.

Its song is a continuous repetition of the syllables, "*John Pierre oh, John Pierre oh, mi yes, mi yes, mi yes,*" with the stress on "*Pierre*" and "*mi,*" with a peculiar intonation, suggesting that of the Scarlet Tanager (*Piranga erythromelas*).

The nest resembles that of the preceding species, and is generally placed in a tree with dark foliage. The eggs are, as in case of the preceding bird, three in number, dull green spotted with reddish brown, the spots being rather larger than in the eggs of *M. gymnophthalma.*

Myadestes sibilans (Lawr.). Soufrière-bird.— Lister says: "I met with this interesting bird on the Soufrière, and in every part of the high woods that I explored. Its song, which causes even those who care little for bird music to pause and listen, appears to be similar to that of a closely allied species, so well described by Mr. Gosse in his account of the birds of Jamaica. During the month of August I noticed that the birds did not sing their full song, but after giving a few notes would stop and give utterance to a harsh note, which reminded me of the discordant one which occurs in the song of the Greenfinch (*Ligurinus chloris*)."

Mr. George Durrant, of Georgetown, St. Vincent, who is well acquainted with this species, tells me the song resembles the syllables: "*I cook' my rice', I put' it out', flam', flam, flam'.*"

Although commonly supposed on St. Vincent to have been confined to the Soufrière, this bird occurred on all the higher ridges of the island. Mr. G. Whitfield Smith, who has taken many of them, tells me that they were particularly numerous on and about the summit of Mt. St. Andrew. I found no trace of it.

Cinclocerthia ruficauda tenebrosa Ridgw. Trembleur. — Ober says of this bird: "Not so abundant as in the woods of Dominica, but still plentiful." Lister writes: "Not uncommon in the high woods. I never saw one on cleared land." I failed to find this bird, but it may still exist in certain remote localities.

Cinclocerthia sp. Quaking Thrush.— Ligon (**1763**, p. 60, "Thrush"; **1764**, p. 101, "Grive"), Hughes (**1750**, p. 72, "The Quaking Thrush"), and Schomburgk ('**48**, p. 681, "*Turdus jamaicensis*"), give a bird evidently of this genus as occurring on Barbados.

Mimus polyglottos orpheus (Linn.). GREATER ANTILLEAN MOCKINGBIRD.— This species has recently been introduced into Barbados from Jamaica but does not yet appear to have become established.

Mimus gilvus (Vieill.). MOCKINGBIRD; PIED CARREAU.— On St. Vincent this bird is very common about Kingstown. It occurs throughout the Kingstown valley, and sparingly along the leeward coast to Chateaubelair. It is most abundant in the town of Kingstown, and in the Botanic gardens.

It occurs on all the Grenadines, and is there the commonest bird; on Grenada it is found abundantly everywhere (except in the deep woods), and is rather partial to neglected pastures.

The nest is rather coarse, of twigs, lined with finer twigs, midribs of leaves, etc., and is usually placed rather low. The eggs are usually three, pale olive or dull green, some very light, others dark, with spots, blotches, or a ring about the larger end, of brown. It is seldom that two eggs are found alike, even in the same set. I have seen a specimen (in the collection of Mr. John Grant Wells) immaculate, except for one or two small and very pale spots.

This species was introduced into Barbados from Grenada in May, 1901, and in the following spring one pair nested near the Garrison at Hastings, and another in the neighborhood of Chelston, the residence of Sir Daniel Morris.

Allenia albiventris (Lawr.). SPOTTED GRIEVE.— The name *Turdus montanus* given by Lafresnaye to this species (Rev. zool., May, 1844, p. 167) is preoccupied by *Turdus montanus* Voigt, (Thierreich, vol. 1, p. 484, 1831; Audubon, Orn. biog., vol. 4, p. 487, 1838, and Townsend, Journ. acad. nat. sci. Phila., 1839, p. 153). Lawrence's name of (*Margarops*) *albiventris* will therefore have to be used (*vide* Riley, : 04b, p. 288).

This bird is rather uncommon on St. Vincent. It occurs about the Queensberry estate in the upper Buccament valley, but is only casually met with at other points, although I have seen or heard it in many places in the woods from Chateaubelair to Kingstown. I obtained one in the Botanic gardens at the latter place, another at Edinboro', and a third at Peter's Hope.

Although Lister says it is never met with out of the high woods, I have most frequently found it in scrubby growth, or on the borders of woodlands. He gives it as not so commonly met with as *Cinclocerthia ruficauda tenebrosa*, but, he writes, "it may be common."

After the hurricane of 1898, this species appeared in numbers on Union Island and Carriacou, where it was resident, according to Wells, as late as 1902. I made a particular search for it during my stay on those islands, but did not find it and therefore, as in life it is a rather noticeable bird with a loud and characteristic note, am forced to the conclusion that it has since died out, as I explored both islands very thoroughly.

On Grenada it is not common, and appears to be confined to the higher wooded parts of the island.

Cory ('92, p. 121) gives this species as occurring on "Lesser Antilles [no.] 33 [= Barbados]"; probably this is a misprint for no. 32 (= Grenada), which locality is omitted.

The notes of this species are clear and loud, resembling the syllables "*whéou whéou whéou*" rapidly repeated half a dozen times or so, sounding much as if someone were calling a dog. In general it keeps near, but not on the ground, and its actions resemble those of thrashers (Toxostoma). Its attitude is very characteristic; the head is kept low, and the tail usually straight up in the air, or slightly inclined over the back. The yellow irides are very noticeable.

Allenia sp. "WREN." — Hughes (**1750**, p. 73, "The Wren") and Ligon (**1763**, p. 60, "Wren"; **1764**, p. 101, "Roytelet") mention a bird, apparently of this genus, as occurring on Barbados.

Margarops fuscatus densirostris (Vieill.). MOCKING THRUSH.— Dr. C. J. Manning obtained a male of this species in his garden at Bagatelle, Barbados, on March 2, 1889. There are no other records.

Margarops sp. "THRUSH."— Hughes, (**1750**, p. 72, "Thrush"), Ligon, (**1763**, p. 60, "Counsellor; **1764**, p. 102, Conseiller"), and Schomburgk ('**48**, p. 681, "*Turdus mustelinus*") mention what appears to have been a species of this genus as occurring on Barbados.

DOUBTFUL SPECIES.

Anas obscura Gmel. BLACK DUCK.— Schomburgk ('**48**, p. 682) mentions this species as a visitor occurring on Barbados. As no one else mentions it, and as none of the Black Ducks have

been recorded in recent years from the West Indies, except Jamaica and Cuba, the record seems rather doubtful.

Dendrocygna arborea (Linn.). Tree Duck; Whistling Duck.— Schomburgk ('**48**) gives this bird from Barbados. There are no records for *D. arborea* from Barbados, although *D. discolor* is reported from there. Possibly this is the species referred to. *D. arborea* has, however, been found on the Bahamas (Andros), Jamaica, Cuba, Haiti, Isle of Pines, Porto Rico, Virgin Gorda, and Barbuda.

Branta canadensis (Linn.). Canada Goose.—Sir Hans Sloane (**1707**, vol. 1, p. 34; **1725**, vol. 2, p. 323) says under *Anser canadensis* Willughb.: "I saw here [Barbados, vol. 1] the Wild Goose of New England, or Geese White and Gray of *Escarbot*, *Nova-Francia*, p. 90: Geese of *Hudson Purchas*, p. 602; of *Saris* ib. 373. Wild Geese of *Copland*, p. 466, who observed the same at the Cape of Good Hope [!]. Of *Payton*, who saw them in an Isle of Ethiopia 33° 30′ lat. 487." Also (vol. 2): "I saw some of these at Barbadoes; they come from the north parts of America, and I think are better meat than the tame ones."

Numenius longirostris Wils. Long-billed Curlew.— Ober gives thus species from St. Vincent, saying that he learned of its occurrence while on that island. It has never been taken except on Jamaica and Cuba.

Ajaia ajaia (Linn.). Roseate Spoonbill.— Lawrence quotes Ober as saying that this bird is of casual occurrence on Grenada. Were this so, Wells, who lived on Grenada all his life would certainly have mentioned it.

Hypothetical Species.

The Cotton-tree Bird.— Hughes (**1750**, p. 72) says: "This is a yellowish bird, about the bigness of a small sparrow; and is chiefly to be found among cotton trees." Possibly the bird referred to is *Dendroica striata*.

Tachornis phoenicobia.— Schomburgk refers to some bird under this name as occurring in Barbados. Possibly it was one of the swifts (Chaetura) that occur in the neighboring islands.

Amazona barbadensis (Gmel.). Barbados Parrot.— Sir

Hans Sloane (**1707**, vol. 1, p. 34) says: "Turner (ap. Purchas, p. 1265) found Hogs, Pigeons, and Parrots here [Barbados]." This is the only statement I can find of their occurrence on that island by a person who actually visited the place. Albin (Nat. hist. birds, vol. 3, p. 11, pl. 11, 1738, "The Barbados Parrot"), Edwards (Birds, vol. 4, p. 162, 1751, "The Great Green Parrot from the West Indies" [Barbados]; *t. c.*, p. 246, "*Psittacus viridis major occidentalis*"), Latham (Gen. syn., vol. 1, p. 284, no. 90, 1781, "The Ashfronted Parrot" [Barbados]; Gen. hist., vol. 2, p. 238, 1822), Brisson (Orn., vol. 4, p. 236, 1760, "Le Perroquet des Barbades .... *Psittacus Barbadensis*"), and Gmelin (Syst. nat., vol. 1, p. 339, 1788, "*Ps*[*ittacus*] *barbadensis*") give a parrot of the genus Amazona as having inhabited Barbados. The species as described is referable in all cases to varieties of *A. aestiva* or *A. ochroptera*. Possibly there was an Amazona allied to these species on the island at the time of its colonization, but there is no definite proof that such was the case. A species of the *A. amazonica* group (to which *A. aestiva* and *A. ochroptera* belong) is common (*A. amazonica*) on Tobago and on Trinidad.

There is a single passing reference to a parrot on Grenada, Dutertre (**1667**, vol. 2, p. 249) saying that the macaw on Guadeloupe is larger than "the large parrots of Guadeloupe or Grenada." Possibly Tobago is meant.

Species Known to Breed.

Barbados.

Puffinus lherminieri Less.
Butorides virescens maculata (Bodd.).
Gallinula galeata (Licht.).
Fulica caribaea Ridgw.
Zenaida zenaida aurita (Temm. and Knip.).
Columbigallina passerina trochila (Bonap.).
Sericotes holosericeus (Linn.).
* *Bellona cristata emigrans* (Lawr.).
Tyrannus dominicensis rostratus (Scl.).
* *Elaenea martinica barbadensis* (Cory).
* *Hologuiscalus fortirostris* (Lawr.).

* Peculiar to the island.

* *Pyrrhulagra barbadensis* (Cory).
Tiaris bicolor omissa (Jard.).
Vireosylva calidris barbadense Ridgw.
* *Coereba barbadensis* (Baird).
* *Dendroica capitalis* (Lawr.).

Introduced.

Sicalis arvensis luteiventris (Meyen.).
Mimus gilvus (Vieill.).
Merula gymnophthalma (Cab.).

ST. VINCENT.

Phaethon aethereus Linn.
Florida caerulea caerulescens (Lath.).
Butorides virescens maculata (Bodd.).
Nyctanassa violacea (Linn.).
Buteo antillarum Clark.
* *Urubitinga anthracina cancrivora* Clark.
Ionornis martinica (Linn.).
Gallinula galeata (Licht.).
Columba squamosa Bonn.
Columbigallina passerina trochila (Bonap.).
Geotrygon montana (Linn.).
Coccyzus minor vincentis Clark.
Crotophaga ani Linn.
* *Amazona guildingii* (Vig.).
Strix nigrescens Lawr.
Cypseloides niger (Gmel.).
Chaetura acuta (Gmel.).
Chaetura poliura (Temm.).
Eulampis jugularis (Linn.).
Sericotes holosericeus (Linn.).
* *Bellona exilis ornata* (Gould).
Tyrannus dominicensis rostratus (Scl.).
Myiarchus tyrannulus tyrannulus (Müll.).
Elaenea martinica flavogastra (Thunb.).
Elaenea martinica martinica (Linn.).
* *Holoquiscalus dispar* Clark.
* *Pyrrhulagra noctis crissalis* Ridgw.
Tiaris bicolor omissa (Jard.).
Euphonia flavifrons viscivora Clark.

* Peculiar to the island.

* *Calospiza versicolor* (Lawr.).
Progne dominicensis (Gmel.).
Vireosylva calidris barbadense Ridgw.
* *Coereba atrata* (Lawr.).
† * *Catharopeza bishopi* (Lawr.).
* *Troglodytes musicus* (Lawr.).
* *Cinclocerthia ruficauda tenebrosa* Ridgw.
Mimus gilvus (Vieill.).
Allenia albiventris (Lawr.).
? Cinchlerminia sanctae-luciae (Scl.).
Merula gymnophthalma (Cab.).
Merula nigrirostris (Lawr.).
* *Myadestes sibilans* Lawr.

THE GRENADINES.

Podilymbus podiceps (Linn.). Carriacou; Isle Ronde.
Puffinus lherminieri Less.[1]
Phaethon aethereus Linn.
Sula cyanops (Sundev.). Kick-'em-Jenny.
Sula leucogastra (Bodd.).
Sula piscator (Linn.).
Fregata aquila (Linn.).
Florida caerulea caerulescens (Lath.).
Butorides virescens maculata (Bodd.).
Nyctanassa violacea (Linn.).
Querquedula discors (Linn.). Isle Ronde.
Erismatura jamaicensis (Gmel.). Isle Ronde.
Buteo antillarum Clark. Bequia.
Ionornis martinica (Linn.).
Gallinula galeata (Licht.).
Fulica caribaea Ridgw.
Larus atricilla Linn.
Sterna maxima Bodd.
Sterna dougalli gracilis (Gould).
Sterna fuliginosa (Gmel.).
Sterna anaethetus (Scop.).
Anous stolidus (Linn.).
Columba squamosa Bonn.
Zenaida zenaida aurita (Temm. and Knip.).
Zenaida vinaceorufa Ridgw. Carriacou.
Columbigallina passerina trochila (Bonap.).

* Peculiar to the island.
† Genus peculiar to the island.
[1] Unless otherwise specified the birds breed in all suitable localities.

Coccyzus minor minor (Gmel.).
Crotophaga ani Linn.
Strix nigrescens Lawr. Bequia.
Sericotes holosericeus (Linn.).
Bellona cristata cristata (Linn.).
Tyrannus dominicensis rostratus (Scl.).
Myiarchus tyrannulus tyrannulus (Müll.).
Elaenea martinica flavogastra (Thunb.). Bequia; Mustique.
Elaenea martinica martinica (Linn.).
Molothrus atronitens Cab. Canouan and southward.
Holoquiscalus luminosus (Lawr.).
Tiaris bicolor omissa (Jard.).
Progne dominicensis (Gmel.). Canouan; Carriacou.
Vireosylva calidris barbadense Ridgw.
Coereba wellsi Cory. (Normal color phase only, = *morrisi* Clark).
Dendroica ruficapilla (Gmel.). Prune; Union Island; Carriacou.
Mimus gilvus (Vieill.).
Merula gymnophthalma (Cab.).

Introduced.

Ortalis ruficauda Jard. Bequia; Union Island.
Eupsychortyx sonninii (Temm.). Mustique.
Numida meleagris Linn. Balliceaux.

Grenada.

Podilymbus podiceps (Linn).
Puffinus lherminieri Less.
Phaethon aethereus Linn.
Florida caerulea caerulescens (Lath.).
Butorides virescens maculata (Bodd.).
Nyctanassa violacea (Linn.).
Falco sparverius caribbaearum (Gmel.).
Buteo antillarum Clark.
Regerhinus uncinatus (Cass.).
Ionornis martinica (Linn.).
Gallinula galeata (Licht.).
Fulica caribaea Ridgw.
Sterna maxima Bodd.
Sterna dougalli gracilis (Gould).
Anous stolidus (Linn.).
Columba squamosa Bonn.
Zenaida zenaida aurita (Temm. and Knip.).

Zenaida vinaceorufa Ridgw.
* *Engyptila wellsi* Lawr.
Columbigallina passerina trochila (Bonap.).
Geotrygon montana (Linn.).
Coccyzus minor minor (Gmel.).
Crotophaga ani Linn.
Strix nigrescens Lawr.
Chaetura cinereiventris guianensis (Hart.).
Chaetura poliura (Temm.).
Glaucis hirsuta (Gmel.).
Sericotes holosericeus (Linn.).
§ *Bellona cristata cristata* (Linn.).
Tyrannus dominicensis rostratus (Scl.).
Tyrannus melancholius satrapa (Licht.).
Myiarchus tyrannulus tyrannulus (Müll.).
Elaenea martinica flavogastra (Thunb.).
Molothrus atronitens Cab.
§ *Hologuiscalus luminosus* (Lawr.).
* *Pyrrhulagra noctis grenadensis* Cory.
Tiaris bicolor omissa (Jard.).
Sporophila gutteralis (Licht.).
Volatinia jacarini splendens (Vieill.).
Euphonia flavifrons viscivora Clark.
Calospiza cucullata (Swains.).
Progne dominicensis (Gmel.).
Vireosylva calidris barbadense Ridgw.
* *Coereba wellsi* Cory. (Black color phase only, = *wellsi* Cory)
Dendroica ruficapilla (Gmel.).
* *Troglodytes grenadensis* (Lawr.).
Mimus gilvus (Vieill.).
Allenia albiventris (Lawr.).
Merula gymnophthalma (Cab.).
Merula nigrirostris (Lawr.).

* Confined to the island.
§ Confined to Grenada and the Grenadines.

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ANATOMY OF *BOOPHILUS ANNULATUS* SAY.

By S. R. Williams.

BOSTON:

PRINTED FOR THE SOCIETY.

October, 1905.

No. 8.—ANATOMY OF *BOOPHILUS ANNULATUS* SAY.

BY S. R. WILLIAMS.

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Introduction.

For many years the cattle disease, Texas fever or redwater, has been under more or less careful observation in the southern part of the United States. Since the tick, *Boophilus annulatus*, has been demonstrated to be the source of infection for this disease it has received its share of attention. Its habits, life history, and external anatomy have been described at length. No description of its internal anatomy, however, has been published.

In the last few years the discovery of the full history of malaria renders it probable that the Sporozoa which cause many of our diseases, Texas fever among others, will be found in altered form in a second host from which the first species must be re-infected. We know that the tick is the alternate host for this parasite, and any contribution to a clear knowledge of its anatomy must be of use in the future tracing out of the portion of the life cycle of the fever-producing organism which is passed in or on the Texas fever tick.

There is much literature on the group of ticks as a whole, but the different families vary so exceedingly in type that a description of one species will not hold for a closely related form. For example, the most considerable paper on a near relative of Boophilus, that of Pagenstecher ('61) on *Ixodes ricinus*, the castor bean tick, shows that Ixodes differs greatly from *Boophilus annulatus* in almost every organ.

I wish to thank Prof. Mark Francis, of the Texas agricultural and mechanical college, for the material studied.

Material and Methods.

I received from Dr. Francis the gravid females, immature females, and males. Some of the gravid females laid eggs in the box in which they had been sent; others oviposited in the laboratory.

The animals were killed in hot water, Perenyi's, corrosive-acetic,

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Carnoy's, and Hermann's fluids. If there is any choice in these fixing reagents the two last are the best. The cells are perhaps a little shrunken after the Carnoy's fluid, but they stain very brilliantly. It proved exceedingly difficult to cut sections of the animal however fixed. The difficulties are two-fold: first, to cause the fixing, dehydrating, and imbedding substances to penetrate successfully the thick chitinous skeleton, and secondly, to cut the chitin even when penetration is complete. The usual substitute for a section is some ragged pieces of chitin and a hole in the paraffin. Collodionization of each section, as recommended by Salmon and Stiles (:02, p. 381) met with no success, especially with the large specimens.

Lest standing in alcohol make the sectioning more difficult, one lot of material was killed and carried as rapidly as possible through the reagents and into paraffin, where some specimens remained a few minutes and others seven days. Neither of these cut any better than others not so treated.

Series which were serviceable for study of the general form of some of the organs were obtained by dissecting off the cuticula from museum specimens which had been in alcohol for ten years. The chitin seems to be free to some extent from the hypodermis in such specimens. Of course the cytological condition of such series is poor, but the sections are complete and perfect series are easily obtained. Each of the few complete series from fixed material was obtained from an animal which was nearly ready to moult, as was shown on examination of the sections. The outer shell was free from the animal and so its breaking did not injure the tissue within the thin and soft new chitin. Moreover, a more thorough penetration of all the fluids was made possible through the holes and pores in the old, loosened cuticula.

I would suggest that where sections are to be made through adult female ticks, they should be fixed in some warm fixing mixture and then left in strong alcohol some days to shrink away from the cuticula. After this treatment the chitin can be dissected off with fine needles, under a dissecting microscope, without serious injury to a great proportion of the specimens, and sections can be made as usual.

The male skeleton is nearly as thick as that of the female, and being smaller, is more difficult to remove, and this method may prove impracticable for males.

Henking ('82) found that in sectioning Trombidium the fat was the disturbing element and he recommends imbedding that species in paraffin, cutting the animal in half, dissolving the fat out with ether, and then reimbedding and sectioning as usual.

Given satisfactory sections, one may proceed with any of the regular processes of staining and mounting. Mayer's alcoholic cochineal, old formula, gave good results. Heidenhain's and Delafield's haematoxylins were also used. Henking used Grenacher's borax carmine for Trombidium.

The work of Pagenstecher ('61) gives a comprehensive review of the literature on Ixodes up to that time. As a complete bibliography of the tick literature is given by Salmon and Stiles (:02) in the "Report of the Bureau of animal industry for 1900," only those papers directly referred to will be included in the present bibliography.

External Form.

The adult; gravid female Boophilus is about half an inch in length and rounded in body. Its legs seem short and its capitulum seems very small, though it is much larger than that of the male. There is a small shield or scutum back of the capitulum on the dorsal side. The genital pore is on the ventral side of the body in the midline between the coxae of the first pair of legs. Behind the fourth pair of legs are the two stigmata or openings of the tracheal system. In the ventral midline and back of this transverse plane lies the anal opening which is closed by a sort of valve.

The male is much smaller than the female and flatter in body. Its beak or haustellum is actually shorter than that of the female, though the proportions make both this and the legs seem longer. The shield in the case of the male covers nearly the whole dorsal surface. There are also four chitinous projections on the ventral side at the posterior end of the male animal which do not appear on the female.

Fig. 1 (pl. 18) is drawn from a natural-sized photograph of a few eggs, a male, and a gravid female, to show their relative sizes.

In fig. 2 (pl. 18) the beak of a small female is drawn as seen from the dorsal side. Just above it is the piece of cowhide which came off with the tick. The haustellum or beak which is composed of

the chelicerae or mandibles with their sheaths and digits (pl. 18, fig. 2, *md. sh.*, *md. dig.*) together with the hypostome or radula is forced into the hide of the host. When the beak has imbedded itself the mandibular digits are set at an angle with the mandibles by muscular action much as the points of a double-pointed harpoon are set in a load of hay. Thus the animal is firmly locked to its host so that the body of the tick is removed only by tearing loose from its capitulum or, as in this case, by removing a piece of the epidermis of the host.

The bit of skin from the host has the appearance of the cone of a volcano as seen from above. The opening (pl. 18, fig. 2, *or. haus.*) is just the size of the anterior end of the beak. On either side of the elevation forming the cone is a shallow depression where the end of the corresponding palpus fits.

The beak is like a rasp, with the mandibular teeth making its sharp point. The eight rows of backward-pointing teeth on the hypostome make the coarse side of the rasp, while the very small points on the dorsal side of the mandibular sheaths make the fine side. The hooked feet of the tick serve to hold the animal in place while it forces in this weapon.

The palpi (pl. 18, fig. 2, *pal.*) lie one on each side of the mandibles. These are four-jointed and have many hairs over their surface. On the dorsal side of the capitulum near its base are found in the female tick two oval areas, the porose areas (pl. 18, fig. 2, *por. ar.*), which consist of a number of slight elevations each with a slit or pit at its apex. A pair of similar or smaller organs, the dorso-submedian porose plates, are found symmetrically placed on the back of the animal just behind the head shield. One of these is shown (pl. 18, fig. 3, *d. sub-med. por. pl.*), together with the marking on the surface of the surrounding cuticula. The round openings in the cuticula in this figure represent either the mouths of glands or the location of surface hairs or bristles (compare pl. 21, fig. 16, *cta.*).

The whole surface is irregularly marked with very fine striae. Secondarily the cuticula is thrown into irregular undulations to conform with organs within. It is depressed along certain definite lines where the internal musculature is attached.

The cuticula in section (pl. 20, fig. 12; pl. 21, fig. 16, *cta.*) is from $\frac{1}{10}$ to $\frac{1}{4}$ mm. thick. It is made up of two portions: an outer, more deeply pigmented layer, and an inner, pale layer. This inner layer

is marked either distinctly or indistinctly with fine vertical lines, and sometimes also shows longitudinal striation. Although the vertical lines cannot be seen to pass through the opaque outer layer, in ticks which have not lately shed or at sharp bends of the cuticula in almost all specimens, the outer layer opens in crevasses or cracks which match the lines seen on the surface in fig. 3 (pl. 18).

The cuticula, then, is traversed by numerous openings for glands and for hairs, by four porose areas in the case of the female, by two spiracles or stigmata, and by the oral, genital, and anal openings.

A section through the stigmatic plate (pl. 18, fig. 5), taken on one side of the stigmal opening, shows the arching cover over the air space beneath supported by numerous pillars of chitin. These pillars cut off small chambers above the hypodermis which may possibly connect with the central air space and increase its capacity.

At this stage in the description it will be useful to introduce a frontal section of a small female (pl. 18, fig. 4), to show the general relationship of the internal organs. The capitulum was bent downward out of the plane of section. The palpi, brain, one of the salivary ducts and many of the individual salivary glands, the region of the ovary and genital passages, the stigmata, and the accumulation of excreta in the renal sac are shown as they lie in the animal.

Musculature.

The musculature of the tick is definitely related to the shapes of the internal organs, especially the alimentary canal and the excretory system.

The most evident systems of muscles are dorso-ventral. These, by their insertion on the ventral side of the body make in the female the two diverging lines on the ventral cuticula which can be followed from the corners of the genital opening backward to the postero-lateral portions of the abdomen. A shorter row of similar dorso-ventral muscle fibers extends in the midline from the anal opening to the posterior edge of the abdomen. The insertion of these systems of fibers on the dorsal side of the animal is not so regular and produces various patterns on the slightly collapsed abdomens. The postanal row is made up of straight dorso-ventral fibers, but those in the lateral rows may slant toward the front before they are inserted on the dorsal wall.

On each side in the region of the coxae there are masses of dorso-ventral muscles. The chief muscles here, however, are those which originate on the dorsal and on the ventral walls and serve to move or fix the coxae. Many of these are long and pass inward to take their origin on the dorsal shield near the origin of the two strong bundles of mandibular muscles.

In the male the lines on the dorsal shield indicate the place of origin of these muscles to the coxae. The scutum in the female is relatively very much smaller and absolutely somewhat smaller. As the female moves very little, and when gravid never from her place of attachment, there is need for less powerful muscles than in the case of the active male.

There is also a system of longitudinal muscles chiefly along or near the dorsal side of the animal. The two heavy bundles which are inserted on the mandibles and originate in the center of the scutum belong to this group. At the point where these muscles originate, above the brain mass, they are flanked by other longitudinal muscle bundles which pass backward and are inserted on the body wall, back of the stigmata.

The muscle of the beak gives the animal a means of maintaining a rigid hold on the host and is therefore the heaviest muscle in the body. It is possible that the flanking muscles aid these which set the mandibles by making more rigid the posterior edge of the scutum.

Most of the muscles enumerated, by contraction might bring pressure to bear on the tracheae, decrease their containing power, and thus function for respiration as does the diaphragm in man.

The dorso-ventral and longitudinal muscles are useful in the case of the female to decrease the size of the abdomen and thus to force eggs out of the expanded uterus at the time of oviposition. During egg-laying the lines on the abdomen become much deeper and more distinct.

A few bundles of fibers separate from the dorso-ventral rows were spoken of as inserted on each side of the genital opening. These are inserted on the wall of the uterus where it is heaviest and most muscular. A good drawing of this system of fibers is shown by Pagenstecher ('61) in his pl. 2, fig. 6. Other fibers come from the ventral floor of the body cavity on both sides. The shell gland on each side seems to be twined about these uterine muscles to some extent.

These muscle fibers probably function during oviposition, to resist the forward thrust of the uterus by compression from the back of the abdomen. There are no fibers from the ventral wall directly below the uterus and receptaculum seminis but these organs have strong longitudinal muscles inserted on the chitinous ridges just inside the genital pore.

Mouthparts and Alimentary Canal.

The mouthparts are well described by Salmon and Stiles (:02, p. 387–392). They are usually spoken of together as the haustellum or beak, which is made up of the two mandibles, the mandibular sheaths, and the hypostome or radula, with a four-jointed palp on either side. Pl. 18, fig. 6, is from a fairly perfect section through the mouthparts at the level of the third joint of the palpi.

The hypostome (pl. 18, fig. 6, *hyp.*) shows six of the eight rows of teeth which are upon it; the outer tooth is not sectioned on either side. It is due to imperfect sectioning that the epistome or mandibular sheath (*md. sh.*) is not continuous around the mandibles, as each has its own sheath. The section shows the articulation (*art.*) of the fourth and smallest segment of the palpus with the third segment.

At the base of the mandibles the two salivary ducts empty into the small mouth cavity. One of these ducts is shown in fig. 4 (pl. 18, *sal. dt.*). Just in front of the entrance of the salivary ducts we may assume that the alimentary canal begins. For though generally the space between the hypostome and the mandibles is a closed cavity for sucking, yet a separation of these organs would locate the true mouth between their bases.

The esophagus passes posteriorly between the sheaths containing the mandibular muscles as a tube compressed from side to side —in cross section a slit. It bends sharply downward in its passage and as sharply up again to bore through the center of the ganglionic mass (pl. 19, fig. 7, *oes.*). The esophagus enters the ganglion on its antero-ventral margin and leaves it at the postero-dorsal margin. Immediately after emerging from the brain the tube, which must now be known as the stomach or digestive portion of the alimentary canal, enlarges greatly and breaks up into three portions. One portion passes directly toward the right side of the animal, a similar portion toward the left side, while the median, larger tube continues

the intestine posteriorly. As soon as this median division passes the uterus in the female or the seminal vesicles in the male, it gives off downward a small tube that continually decreases in size and goes toward the cloaca. This is shown in the side view of the alimentary canal (pl. 19, fig. 7). The larger part of the median tube continues posteriorly. The further description of the three main branches of the intestine is similar. They each branch into parts — four each in the specimen figured — which end blindly.

For convenience' sake these different diverticula of the alimentary canal have been labeled *1*, *2*, and *3*, beginning from the right side, and their subdivisions have been lettered *a*, *b*, *c*, and *d*. The alimentary canal as seen from above is shown, thus labeled, in fig. 8 (pl. 19). The division is something like that shown in Pagenstecher's figs. 1 and 3, pl. 2, for *Ixodes ricinus*, but differs in the place of origin and the amount of branching of the lateral portions. Pagenstecher represents all the diverticula as radiating from a common center while in Boophilus they arise from the three branches just described.

In fig. 9 (pl. 19) the same alimentary canal is shown as seen from the right side. Diverticulum *1a* is a short one. It turns back on itself and ends blindly, pointing downward; *1b* extends anteriorly outward and downward and crumples up at the limiting boundary, the hypodermis; *1c* extends directly outward and downward, bending forward and then backward, then forward again to end below the midplane of the body; *1d* extends backward as the main portion of division *1*, after giving off caeca *1a*, *1b*, and *1c*, and reaches the posterior end of the animal. Here it bends sharply forward and follows the floor of the body cavity to the anterior end again, where it turns upward and ends blindly above the level of the end of *1c*. This brings out the point indicated by the dotted lines in fig. 7 (pl. 19), that the principal diverticula, *1d*, *2a*, *2b*, *2c*, *2d*, and *3d*, on account of their bending down at the posterior end and extending forward, are from one to one and a half times the length of the body.

These caeca are packed away irregularly as fig. 10 (pl. 19) shows. This is a view of the same alimentary canal as seen from below. The comparative symmetry has disappeared. Neither *1a*, *3a*, nor *3b* was seen at all. The diverticula of the left branch of the canal seem to have extended farther back before turning forward; *3d* is seen to be much farther back than *1d*. Conversely, however, it does not reach to the anterior end of the body cavity.

The tendency seen in *1d* above to pass posteriorly for the second time is accentuated in *2b* and *2c*, the two central diverticula, which turn backward at about the region of the genital organs. The posterior end of the alimentary canal as indicated in fig. 7 (pl. 19) is not to be seen in fig. 10 (pl. 19). This is because in older ticks little or no use is made of the cloacal end of the canal, and so after removal of the anal cuticula in dissection the small broken end of the intestine was not plain.

In the young female the body cavity seems completely filled with the alimentary canal and its diverticula, but as the animal becomes mature the eggs crowd the digestive system to the wall as shown in fig. 22 (pl. 22).

A cross section of a diverticulum of the alimentary canal of an adult female is shown in fig. 11 (pl. 20). The outer layer is connective tissue and within are two sorts of cells: small triangular cells filled with granules which stain deeply with haematoxylin, and large cells of a more homogeneous structure and with nuclei proportionally smaller.

According to Pagenstecher ('61, pt. 2, p. 31) the pigmented cells, which in many cases lie about the alimentary canal, function as liver cells. These pigmented cells, however, seem too sporadic in their distribution in Boophilus to function actively as digestive cells. In many specimens there are none of these irregular pigment masses, while the large intestinal cells contain all the pigment. Since surrounding cells are not always to be seen and since the triangular cells may be assumed to be glandular in function, as they stain so heavily with haematoxylin, I have called them tentatively liver cells (pl. 20, fig. 11, *cl. hep.*).

The large cells with small nuclei and homogeneous protoplasm, which form the main mass of the intestine wall, are certainly the usual digestive cells which line any alimentary canal.

Fig. 12 (pl. 20) is of a section through a diverticulum of the intestine of an adult male. With it are also shown a tracheal tube and a renal tubule. In this cross section the hepatic (?) cells are not so distinct as in the previous one, perhaps because it is stained with a carmine stain. This section illustrates very nicely the stage of ecdysis at which I have been successful in cutting sections. The cuticula (*cta.*) has pulled slightly away from the hypodermal layer (*hy.*), and that which will be the new cuticular layer (*cta'.*) after the

ecdysis, shows as a transparent structureless membrane. The sections are nearly perfect as breaking of the separated cuticula does not tear the tissue.

Salivary Glands.

The tick has paired salivary structures. These lie on each side of the body nearer the anterior end and each is made up of two parts, the duct and the racemose gland. The salivary ducts resemble the tracheae in that they have a striated appearance due to thickenings of the walls. They differ in that the striation of the tracheae is finer and the tracheal branches are long, slender, and twisted, while the branching of the salivary duct is short and comparatively heavy. As has been said, the salivary ducts empty into the hinder part of the pharynx at the base of the mandibles and hypostome. For the duct on the right side see pl. 18, fig. 4, *sal. dt.*

The glandular portion begins in front of the brain and extends to behind the stigmata. The duct and glandular portions together look much like a bunch of grapes (pl. 20, fig. 14). The description and figures given by Pagenstecher show conditions in *Ixodes ricinus* similar to these in Boophilus. In Ixodes, however, the glandular portion is not to be found in front of the brain nor behind the stigmata. In the gravid female Boophilus the egg mass crowds the salivary system forward and to the sides and one preparation indicated a distinct degeneration of the salivary cells. Possibly this is to be correlated with the decrease in size of the anal portion of the intestine and the accumulation of renal concretions in the renal sac and Malpighian tubules. Each part of this racemose gland is separate from all other parts and has its own drainage duct which unites with another and these with others till the main duct is formed.

The number of cells making up one of the glandular divisions is not constant, but there are certainly never more than ten nuclei to be seen and sometimes only one.

Glands of the Skin.

Boophilus has many glands which lie in the hypodermis and open to the exterior through large pores in the chitinous cuticula. There are also passageways for hairs which to a slight extent resemble the

gland ducts. One of these gland ducts leads through the cuticula into an expanded chamber in the hypodermis, the walls of which may show from one to five nuclei. The chamber may extend inward from the cuticula more than twice the average thickness of the hypodermis—in one instance $\frac{1}{5}$ of a millimeter. Fig. 16 (pl. 21) shows two glands and two bits of cuticula, one of which has a gland duct through it and the other a passage for a hair. These glands seem most abundant on the posterior part of the abdomen of the female. They are very variable in shape and in size.

According to Lang ('94, p. 540), glands which do not open in connection with the legs have been considered oil glands, scent glands, poison glands, etc. As an example of the last sort he instances the paired poison glands at the end of the abdomen of the scorpion.

Excretory System.

The excretory system in Boophilus does not correspond to that in *Ixodes ricinus*. In that form as described by Pagenstecher ('61) the organ of excretion consists of two long unbranched tubes of small diameter opening into the cloaca and so entangled with the salivary glands and so coiled that they were to be isolated with difficulty.

According to Kersey ('72) the urinary tubules of *Ixodes dugesii* are blind tubes, subclavate in the fore part of the body, and open into the last part of the intestine, where they form a sort of urinary bladder.

In Boophilus the excretory system is constituted on the plan already outlined by the alimentary canal (compare fig. 8, pl. 19, and fig. 15, pl. 20). Three main divisions, one lying above the origin of the legs on each side and one in the midline, are connected by a cross tube just above and behind the similar cross connection of the alimentary canal.

The main part of these tubes is on the dorsal side of the animal just beneath the hypodermis. Fig. 15 (pl. 20) shows the relations of these divisions. The lateral portions send out small twigs which fit in as best they may above the musculature of the legs and then continue backward, turning with the corresponding intestine diver-

ticula forward again on the ventral side as far as the brain. They send out no branches, however, on the ventral side of the animal.

The median, larger portion, into which the lateral branches connect by the cross tube, must unite in some way, just back of the uterus in the female and the seminal vesicles in the male, to the large sac, which is not seen in the youngest specimens and which in all adults is full of purple-edged, whitish globules. This I have called the renal sac. Just before the renal sac is reached there are two tubes given off at an angle toward the posterior end of the animal. As soon as these tubes reach diverticula *2a* and *2d* of the alimentary canal they follow these diverticula to the posterior end and stop blindly as they reach the region where the intestines turn forward.

Behind the spot where the median tube connects with the renal sac it bifurcates and each section passes back to the posterior of the animal, follows the body wall to the ventral side, then forward again to the region of the ventral end of the renal sac, and each turns outward and ends blindly.

A section across a Malpighian tubule has been shown with that of an intestine diverticulum and a trachea in fig. 12 (pl. 20). There is a very faint, often imperceptible connective tissue layer on the outside. The renal cells are flat with comparatively large nuclei. This differs from the condition in Ixodes only in the comparative size of the nuclei. Pagenstecher says that the nuclei in the renal epithelium are small.

In the older specimens, both male and female, the renal sac and later (pl. 22, fig. 22), the different branches of the excretory system are filled with the opaque, purple-edged globules previously mentioned. These globules, according to both Pagenstecher and Griffith, give the murexide test for uric acid, thus proving the renal function of the system. No clear connection with the outside of the body has been demonstrated. The observed relation of the renal sac to the postintestine is represented in fig. 7 (pl. 19). There may be a free passage in younger specimens, but the steady accumulation of renal material throughout life and the definite order of filling the renal cavities with the renal globules indicates that there is no real amount of excretion.

In a young female the renal tubes are either invisible or visible because outlined by pigment about their walls. In an older tick

the renal sac begins to appear, growing opaque as the spheres of uric acid accumulate in it. As the female becomes more and more distended with eggs the globules begin to fill back into the tubes and their branches, and in the gravid female the whole of the system of tubes is full of this granular deposit.

The diameter of these filled tubules is not constant. In replete forms where each tube can be followed with the naked eye from section to section, the same tube may both disappear in one region and be greatly distended in another.

For the usual conditions of the renal tubules see the cross section of gravid female (pl. 22, fig. 22). The male tubules never become as full of the excretory matter as do those of the female.

Respiratory Organ.

The hexapod larva of Boophilus is reported to have no stigmata and no tracheae. The adult breathing pores, stigmata, or spiracles have been illustrated in section in the general frontal view (pl. 18, fig. 4, *stig.*), and in the discussion of the cuticula (pl. 18, fig. 5). From the air space just within the stigma, the air tubes pass inward in all directions, dividing into smaller and smaller vessels, which twine about all of the internal organs and render gross dissection difficult. There are about eight or ten of the large tubes on each side. This is well shown by Pagenstecher ('61, pl. 1, fig. 9).

The main course of the tracheae is forward in the direction of the brain, salivary glands, branches of the alimentary canal, and genital organs. Each trachea shows a finely cross striate appearance just as do the insect tracheae, due to the alternate thinning and thickening of the tracheal wall. This is much the same appearance as has already been described for the salivary duct. A trachea in cross section is shown in fig. 12 (pl. 20).

According to Lang, Ixodes has that type of trachea which is branched like a tree in the body as in insects and myriapods. The air space just within the stigma of Boophilus represents the tree-trunk, and the eight or ten large tubes leading from this the branches of the tree.

Blood System.

Lang ('94, p. 546) says: "Unter den Acarinen ist ein Herz bis jetzt nur bei Gamasiden und bei Ixodes aufgefunden." Griffith ('92, p. 146) states: "In those Arachnida which breathe only by tracheae the circulatory apparatus is rudimentary, there appears to be a simple dorsal vessel without arteries or veins and it may be remarked that in some species the heart or dorsal vessel appears to be entirely wanting."

In all the tick preparations but one, the latter part of Griffith's statement seemed to hold. In one series of cross sections, however, of a female of about 5 mm. in length, there is a delicate aggregation of flattened cells on the dorsal side of the animal in the median plane just beneath the hypodermis. This mass of cells has an irregular cavity in its center in nearly every section. The cavity is much wider from side to side than dorso-ventrally and the whole indicates a tube much flattened dorso-ventrally, extending posteriorly about a millimeter from the connective tissue sheath surrounding the brain. The ovary in this specimen was immature, so that the diverticula of the alimentary canal and the other organs of the body were not compressed by eggs, and it may be that this elongated tube is the simple dorsal vessel spoken of by Griffith. Since, however, no other series showed these appearances, it may be no indication of a blood system in Boophilus.

Nervous System.

I have little to add to the description of the nervous system as given by Pagenstecher for Ixodes. There is but one large ganglion surrounding the esophagus (pl. 18, fig. 4; pl. 19, fig. 7, *br.*). This is covered by a connective tissue capsule. The cortex of this brain is a thick layer of nuclei of nerve cells and the center is a mass of fibers.

No nervous connection was found between the appearances on the side of the scutum, which are called eyes by Salmon and Stiles, and the brain mass.

The porose areas which have been shown on the dorsal side of the base of the female capitulum (pl. 18, fig. 2, *por. ar.*) are pecu-

liar sense organs which deserve further study. A sagittal section through one of these is shown in fig. 13 (pl. 20). Each one of the slight elevations on the porose area has a pore which extends entirely through the cuticula. Below the pores, conical cells are seen, some of which project slightly into the corresponding pores, very likely in a fresh unshrunken specimen nearly to the surface of the cuticula. These cells have fibers at their proximal ends (pl. 20, fig. 13, *n.*), which form a compact bundle and can be traced backward to the connective tissue capsule of the brain.

As the dorso-submedian porose areas (pl. 18, fig. 3) have exactly the same appearance as the porose areas already described, it is fair to assume that they also have nerve bundles leading to the brain, but these are yet to be demonstrated.

Female Sexual Organs.

The greatest difference between *Ixodes ricinus* as described by Pagenstecher, and *Boophilus annulatus* is in the sexual organs. According to Pagenstecher the plan on which the male and female organs are built is much the same. He figures for each, paired glandular bodies, testes or ovaries, for the preparation of the sexual products, paired canals leading these products into a common receiving and protecting chamber, and an unpaired outlet.

For the female organs in more detail, he shows in his figs. 6 and 11, pl. 2, with a large "Vorhof" next the genital pore to which muscle fibers are attached. A constricted area into which the paired shell glands pour their secretion leads backward from the "Vorhof" and widens out to become the large receptaculum seminis. At the posterior end of this, again separated by a constriction, is the uterus which (Pagenstecher, '61, pl. 2, fig. 11) receives from behind the duct made by the fusion of the two oviducts. The ovaries lie on each side of this central series of unpaired chambers and the oviducts lead from the anterior ends of the ovaries back parallel with them to the point of fusion into a single oviduct behind the uterus.

The male organs are similar except that the very small testes lie forward and the vasa deferentia lead backward from them to the posterior end of the seminal vesicles and empty there separately.

The foregoing description of the female organs of Ixodes would fit much better the organs of the male Boophilus than those of the female. In Boophilus the female organs are not tandem, one following another, but the uterus and receptaculum lie one above the other. There is no condition in Boophilus like that described for the male *Ixodes ricinus.*

The sexual opening or genital pore in Boophilus, instead of lying between the coxae of the last pair of legs as in *Ixodes ricinus,* is between the coxae of the first pair of legs. In the female Texas fever tick the duct leading from the genital pore first extends dorsally and then turns posteriorly. Almost immediately it divides into a dorsal and a ventral portion, and a cross section through the animal in this region (pl. 21, fig. 17) shows the two chambers, one above the other, and the ventral one with its lumen obliterated by the muscular contraction. The wall of this passageway is very thick and is composed of a heavy ring of circular muscle fibers within which the much wider longitudinal fibers are seen (pl. 21, fig. 17, *rec. sem.*).

The two chief rows of dorso-ventral muscles take origin close on each side of the genital pore and genital ducts (pl. 21, fig. 17, *mu.*).

The dorsal passageway (pl. 21, fig. 17, *ut.*) is slightly thinner-walled with a large lumen, but still with strong circular and longitudinal muscles.

Fig. 18 (pl. 21), which is seventy-five micra farther back in the body, shows that the ventral chamber, which has now widened out greatly, acts as the receptaculum seminis, for it is entirely full of ripe sperm.

In this section the walls of the dorsal chamber, the uterus, are much thinner and the enclosed cavity is much larger. The dorsal wall of the uterus contains no muscular tissue at all and is full of nuclei crowded closely together.

The oviducts are very short. The sac-like receptaculum has its posterior corner prolonged on each side into the ovary proper. The transition is abrupt. In one and the same section (pl. 21, fig. 18) one may see the receptaculum (*rec. sem.*), the projection on the right side which shows the beginning of the oviduct (*ovd't.*), and the ovary (*oa.*). Most of this oviduct lies in the section just before this one, but none of the ovary is to be seen in the preceding section.

Before passing to the description of the ovary itself another structure which appears at this level should be described. The paired shell glands are to be seen in section in both figs. 17 and 18, (pl. 21) *sh. gl.* They are much coiled, as the sections show, and empty into the sides of the neck of the uterus at a level anterior to that of the section — in fact just as soon as the uterus is separate from the receptaculum.

The shell gland has about the same diameter throughout its length and the lumen is constant. The nuclei of the cells of this gland stain very deeply in Heidenhain's haematoxylin. The muscle fibers which are inserted on the neck of the uterus have already been described.

The ovary itself is a tube whose wall is made up of one or at most two layers of germinative cells. The turnings and shape of the ovary are difficult to describe, but a comparison of figs. 19 and 20 (pl. 21) and the text figures A and B will aid the description. Beginning at the receptaculum, an upward arch results in elevating the portions of the ovary just back of the uterus above the level of diverticula *1d* and *3d* of the alimentary canal and thus makes the ovary one of the organs just beneath the dorsal hypodermis in the midlength of the animal.

The attachments of the two main rows of the dorso-ventral muscle fibers are to be found both to the outside and to the inside of this part of the ovary since here the ovary flexes sharply toward the sides of the animal. There is also just behind this region a depression of the ovary toward the ventral side of the animal, and the two concavities thus produced permit diverticula *2a* and *2b* of the alimentary canal on one side of the midline, and *2c* and *2d* on the other side to pass over the ovary and so back to their downward bending at the posterior end of the animal (see text figure C, page 332).

The next elevation of the ovary carries its sides, both right and left, over the returning ventral divisions of diverticula *2b* and *2c* and over the ventral branches of the Malpighian tubules.

The posterior portion of each side of the ovary is pressed toward the dorsal wall by the increase in size of the renal sac. It extends forward again some distance over the posterior part of the renal sac and at this point is continuous with the opposite side. If the single ovary be formed from the fusion of the posterior ends of two

formerly separate ovaries — one from each side of the uterus — this would be the region of their fusion, but my preparations show no trace of such a process.

The condition just described is very similar to that figured by Lang ('94, p. 551, fig. 376), for Trombidium on the authority of Henking. In that case, however, the vagina opens posteriorly and the oviducts are shown connecting directly with the uterus.

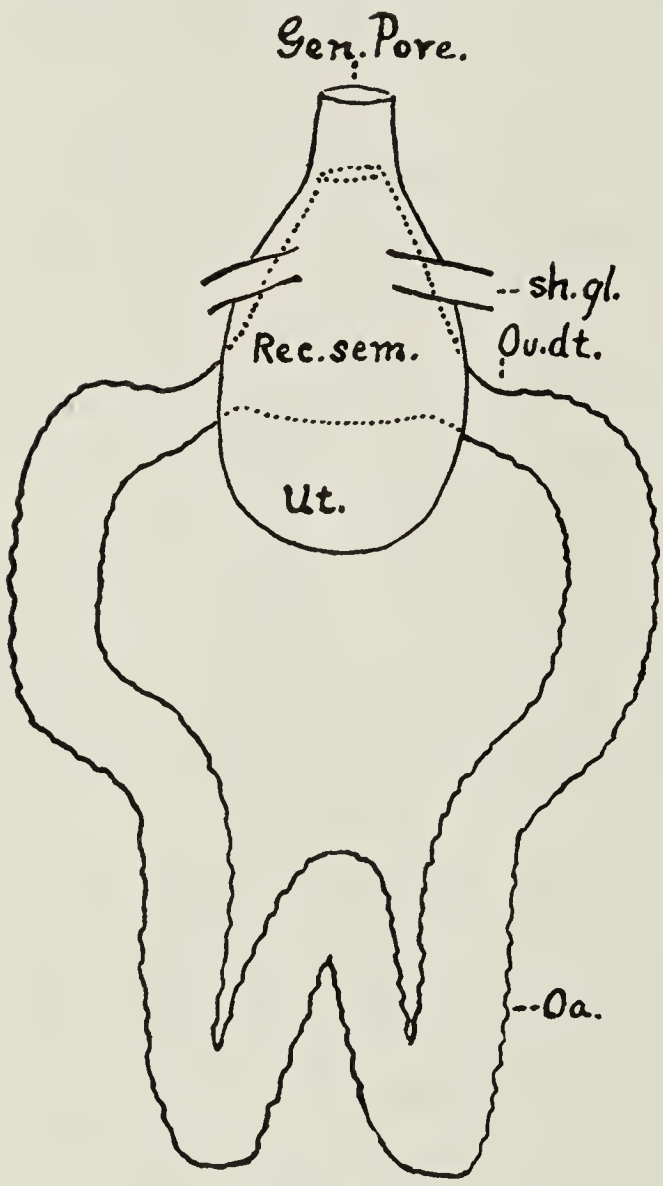

Fig. A.

The shape of the ovary just described is shown by diagram in text figure A. This is drawn as seen from the dorsal side with the receptaculum seminis indicated below the uterus and openings into the uterus for the ducts of the shell glands.

A diagrammatic side view is shown in text figure B. This brings out the relation of the receptaculum to the oviduct, uterus, and shell glands. As the eggs ripen they pass from the ovary into its central cavity, from there through the oviducts to the receptaculum seminis where they are fertilized, and thence to the uterus. There the shell glands are enabled to furnish their secretion and the eggs are stored to wait the time of deposition. The eggs are usually laid in a cluster and this cluster may be a mass larger than the emptied body of the female which produced it.

The tubular condition of the ovary in section with one or at most two layers of germinal cells is shown in fig. 21 (pl. 21), which is a section across the right ovary (*oa. dx.*), the lumen of the ovary indicated (*lu. oa.*), and the eggs (*ov.*), with their especially large nuclei.

Fig. 22 (pl. 22) shows how the gravid female becomes filled with

eggs almost to the destruction of other organs. The alimentary diverticula lie against the outer walls of the body or against supporting muscle fibers. Their cavities are entirely suppressed although the triangular cells, which are assumed to be liver cells (pl. 20, fig. 11, *cl. hep.*), are still evident. The tracheae are proportionately much less important. Only the muscles and the Malpighian tubules with their contents of shining granules occupy large spaces still.

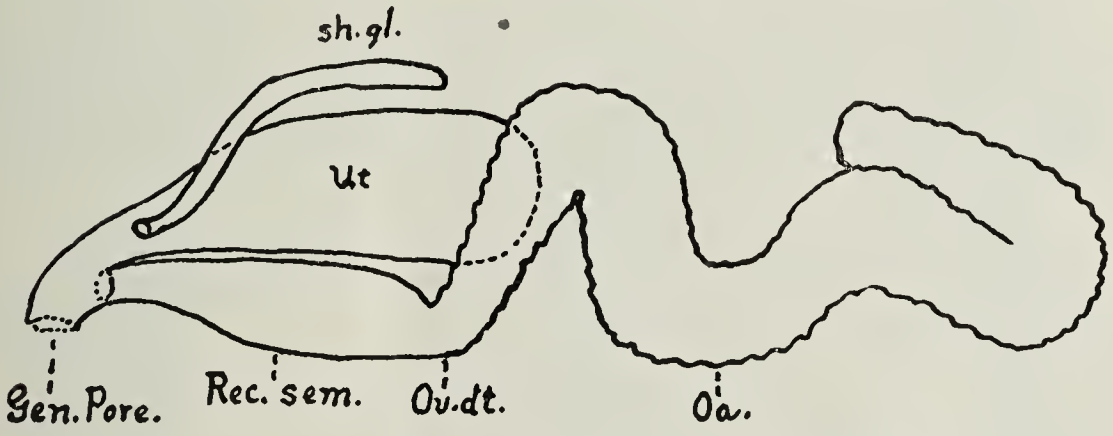

FIG. B.

The Malpighian tubules are larger in proportion to the whole animal and therefore much larger absolutely than in smaller specimens.

One or two of the eggs in this section dropped out and left the cavities as indicated in the figure. Except for these the section is perfect and well illustrates the relative sizes of eggs and other organs.

MALE REPRODUCTIVE SYSTEM.

The male reproductive organs are bilateral and are shaped somewhat like the ovaries of *Ixodes ricinus* as figured by Pagenstecher, but not at all like the male organs figured by him. They also resemble in shape the male organs of Uropoda as reproduced by Lang, ('94, p. 553, fig. 377) after Winkler.

There is first a heavy-walled mass just back of the sexual opening which I have labeled *pe.* (pl. 22, fig. 25) though there is no evidence that it is an extrusible organ. At the sides of this come the vasa deferentia. Posterior to the thick-walled mass in the midline is a system of sacs running as far as the anal opening and with diverticula even farther back. A section shows that these sacs are seminal vesicles (pl. 22, figs. 23, 25, *sem. ves.*). The sperm contained in

these sacs in all the males successfully sectioned was not ripe, whereas that in the receptaculum of the female was always shaped like mature sperm.

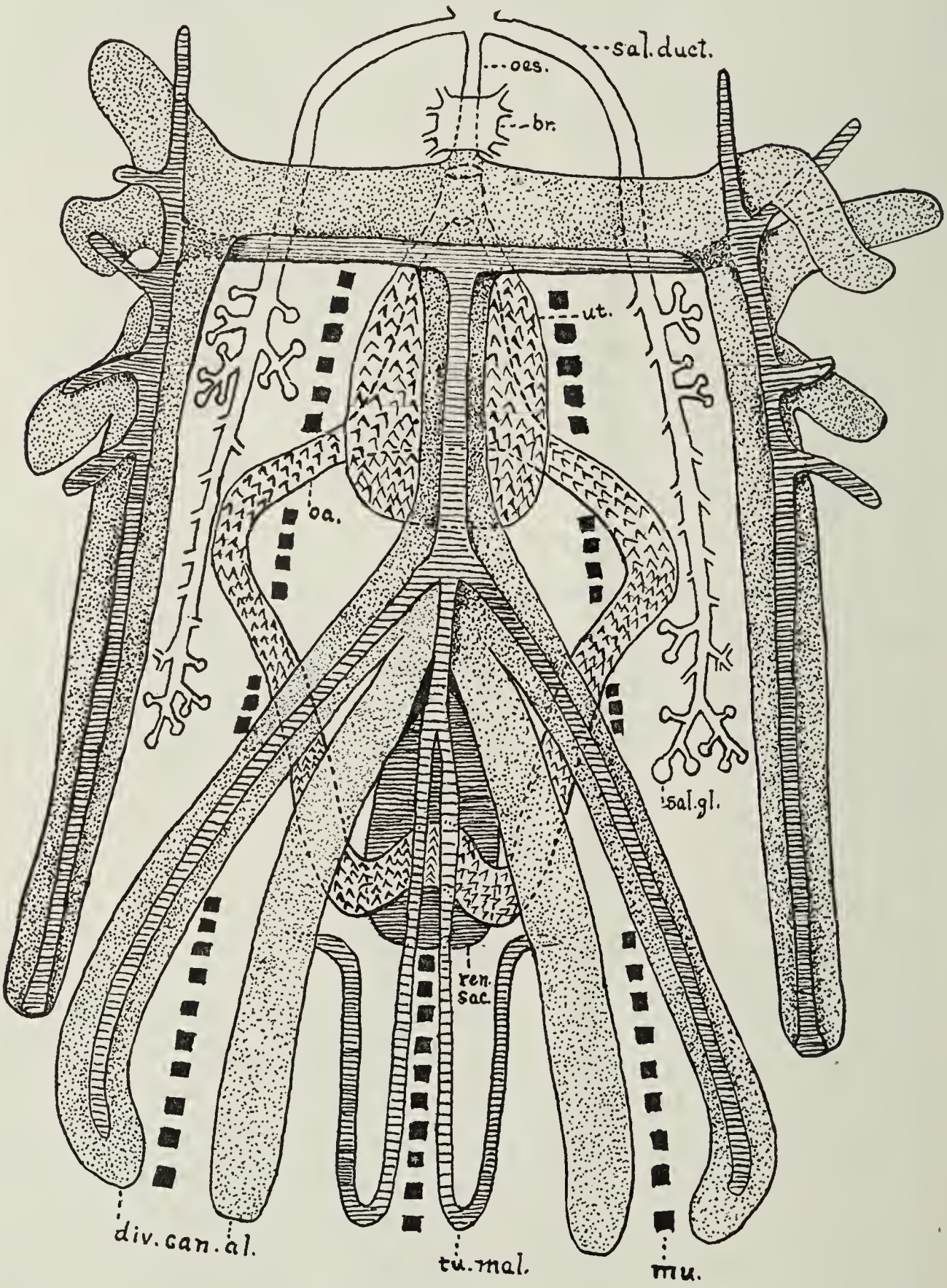

FIG. C.

On each side of this central mass of seminal vesicles lies a testis, an exceedingly large body proportionately, which lies with and

behind the salivary gland complex. A section across a testis (pl. 22, fig. 24) shows five masses of cells ("follicles," Griffith, '92, p. 439) loosely bound by connective tissue. These cells show very large nuclei and are probably the sperm mother-cells. The space between the follicles and the vasa deferentia contains, here and there, the same elongate cells which fill the seminal vesicles and which have been assumed to be immature sperm.

Finally the three systems, digestive, female reproductive, and renal, are put together diagrammatically in text figure C. Each system occupies approximately its relative position and shape. The salivary glands would lie under, around, and over the lateral portions of the alimentary and renal systems, but to avoid complexity the main salivary ducts only are shown.

Summary.

The external porose areas on Boophilus are sense organs with sensory cells in the openings through the cuticula. This cuticula is also perforated by the openings of numerous multicellular glands and hairs.

The alimentary canal is a slightly curved tube passing through the brain and with six large diverticula which occupy most of the body cavity in immature females and males, and are evidently the important digestive regions.

The triangular, heavily stained cells in the walls of these diverticula are suggested as the functional "liver" cells rather than the pigmented cells figured by Pagenstecher.

The salivary glands are paired racemose glands emptying into the mouth cavity.

The excretory system is modeled after the alimentary canal with main diverticula following those of the digestive system and all connecting with a renal sac.

Adult females probably take in little food and eject nothing from the alimentary canal or the renal system.

There is evidence in one case of what may be a simple heart.

The female organs differ in every detail from those of *Ixodes ricinus*. The ovary in Boophilus is a continuous loop from one oviduct to the other, passing backwards around the main alimentary canal.

There is a receptaculum seminis which receives the oviducts and connects with a dorsal uterus. There are paired shell glands emptying into the uterus. Ripe sperm was found in the receptaculum.

The male organs are paired testes, vasa deferentia, and a mass of seminal vesicles in the midline. These vesicles contained no ripe sperm.

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EXPLANATION OF PLATES.

Zeiss microscope, apochromatic objectives, compensating oculars, and camera lucida used where possible.

Abbreviations.

A. Anterior.
art. Articulation.
br. Brain.
cl. div. can. al. Cell of diverticulum of alimentary canal.
cl. hep. Digestive cell.
clo. Cloaca.
cta. Cuticula.
cta'. New cuticula.
D. Dorsal.
d. sub-med. por. pl. Dorso-submedian porose plate.
div. can. al. Diverticulum of alimentary canal.
1a, 1b, 1c, 1d, 2a, 2b, 2c, 2d, 3a, 3b, 3c, 3d. Diverticula numbered from right to left.
gen. pas. Genital passage.
gen. por. Genital pore.
gl. Gland.
hy. Hypodermis.
hyp. Hypostome.
lu. Lumen.
lu. oa. Lumen of ovary.
md. dig. Digit of mandible.
md. s. Left mandible.
md. sh. Mandibular sheath.
mu. Muscle fiber.
n. Nerve.
oa. Ovary.
oa. dx. Right side of ovary.
oes. Esophagus.
or. haus. Opening in skin of host made by beak of parasite.
ov. Ovum.
ovd't. Oviduct.
pal. Palpus.
pal. s. Left palp.
pe. Penis.
por. ar. Porose area.
rec. sem. Receptaculum seminis.
ren. con. Renal concretions in Malpighian tubules.
ren. sac. Renal sac.
sal. dt. Salivary duct.
sal. gl. Salivary gland.
sem. ves. Seminal vesicle.
set. Seta.
sh. gl. Shell gland.
stig. Stigma.
te. dx. Testis, right.
te. s. Testis, left.
tr. Tracheal tube.
tu. mal. d. Malpighian tubule, dorsal portion.
tu. mal. v. Malpighian tubule, ventral portion.
ut. Uterus.
va. df. Vas deferens.
ves. sem. Seminal vesicles.

PLATE 18.

Fig. 1. Drawing of male tick, female tick, and eggs. Natural size.

Fig. 2. Mouthparts of partly grown female, together with the piece of epidermis pulled from the host; oc. 4, obj. 16 mm., tube 145 mm. × 55.

Fig. 3. Cuticle of dorsum showing a "dorso-submedian porose plate"; oc. 4, obj. 8 mm., tube 145 mm. × 120.

Fig. 4. Frontal section to show general relations of organs in a female; oc. 6, obj. (2 in.). × 25.

Fig. 5. Frontal section through spiracle or stigma; oc. 4, obj. 8 mm., tube 145 mm. × 120.

Fig. 6. Cross section of mouthparts; oc. 4, obj. 8 mm., tube 145 mm. × 120.

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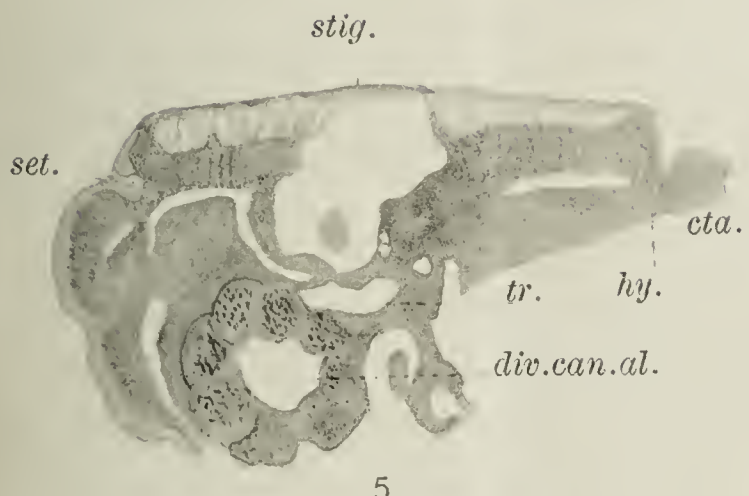

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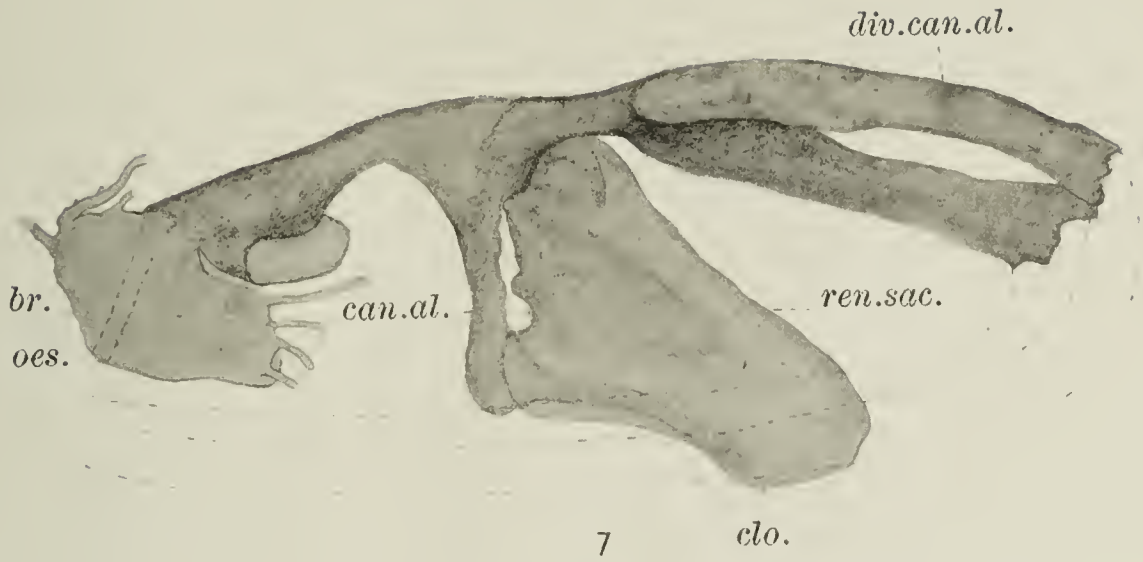
PLATE 19.

Fig. 7. Side view, alimentary canal, small specimen. Spencer microscope ; oc. 1 in., obj. $\frac{2}{3}$. × 75.

Fig. 8. Dorsal view, alimentary canal, adult female ; oc. 4, obj. (2 in.). × 15.

Fig. 9. Side view, same alimentary canal. × 15.

Fig. 10. Ventral view, same alimentary canal. × 15.



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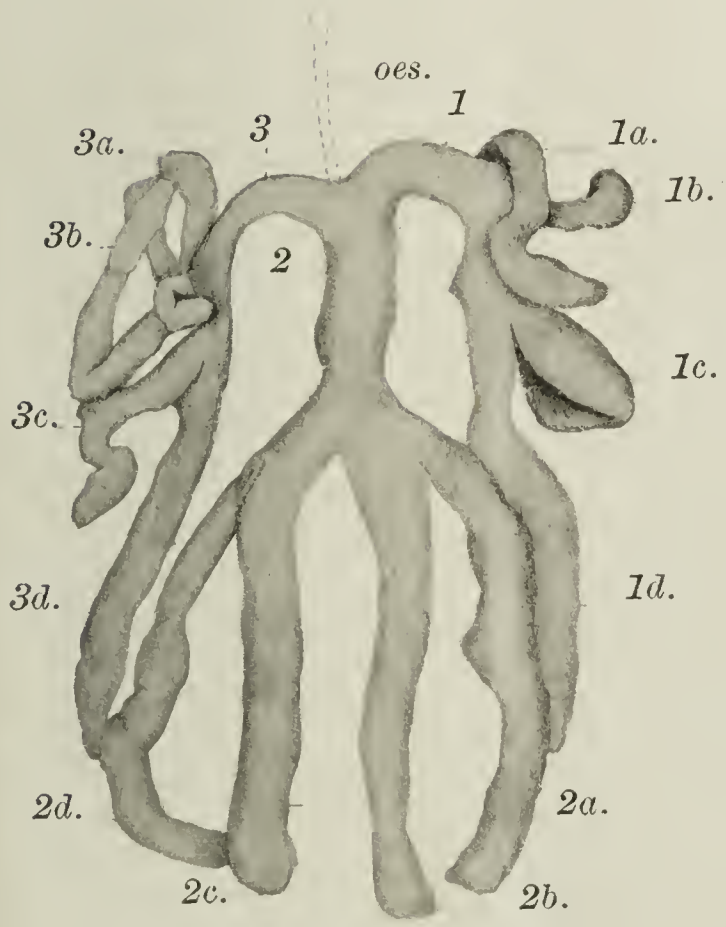

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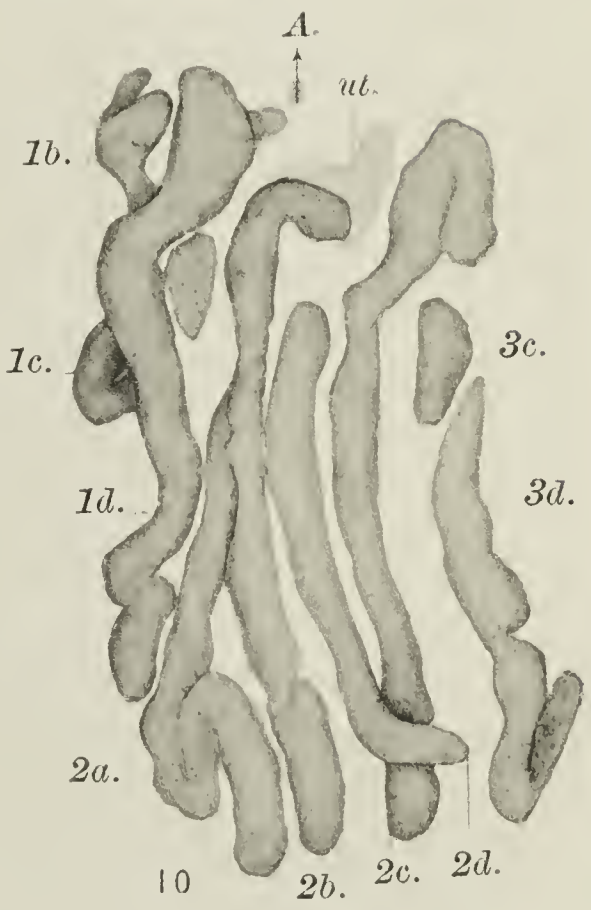

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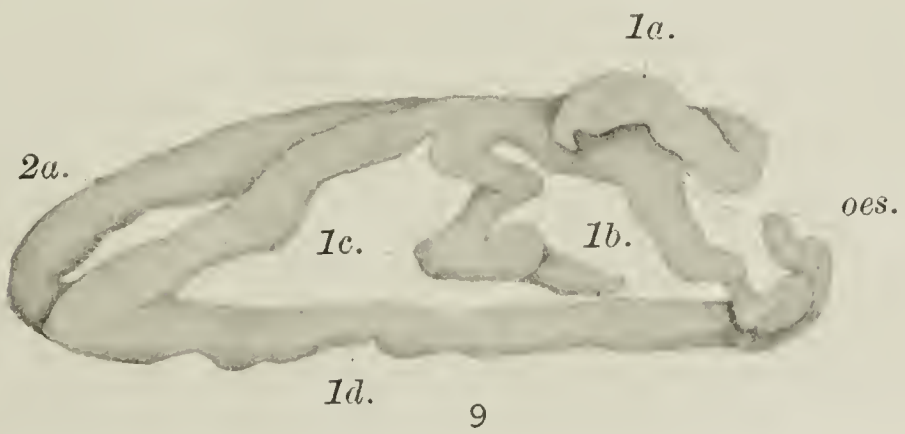

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PLATE 20.

Fig. 11. Cross section of a diverticulum of the alimentary canal. Haematoxylin; oc. 4, obj. 8 mm., tube 145 mm. × 120.

Fig. 12. Cross sections of a diverticulum of the alimentary canal, a trachea, and a Malpighian diverticulum from a male specimen; oc. 4, obj. 4 mm., tube 145 mm. × 225.

Fig. 13. Section through a porose area of a female capitulum from a frontal section; oc. 4, obj. 4 mm., tube 145 mm. × 225.

Fig. 14. View of a small portion of a salivary gland from above; oc. 4, obj. 8 mm., tube 145 mm. × 120.

Fig. 15. Dorsal view of the whole excretory system of a male; oc. 4, obj. 16 mm., tube 145 mm. × 55.

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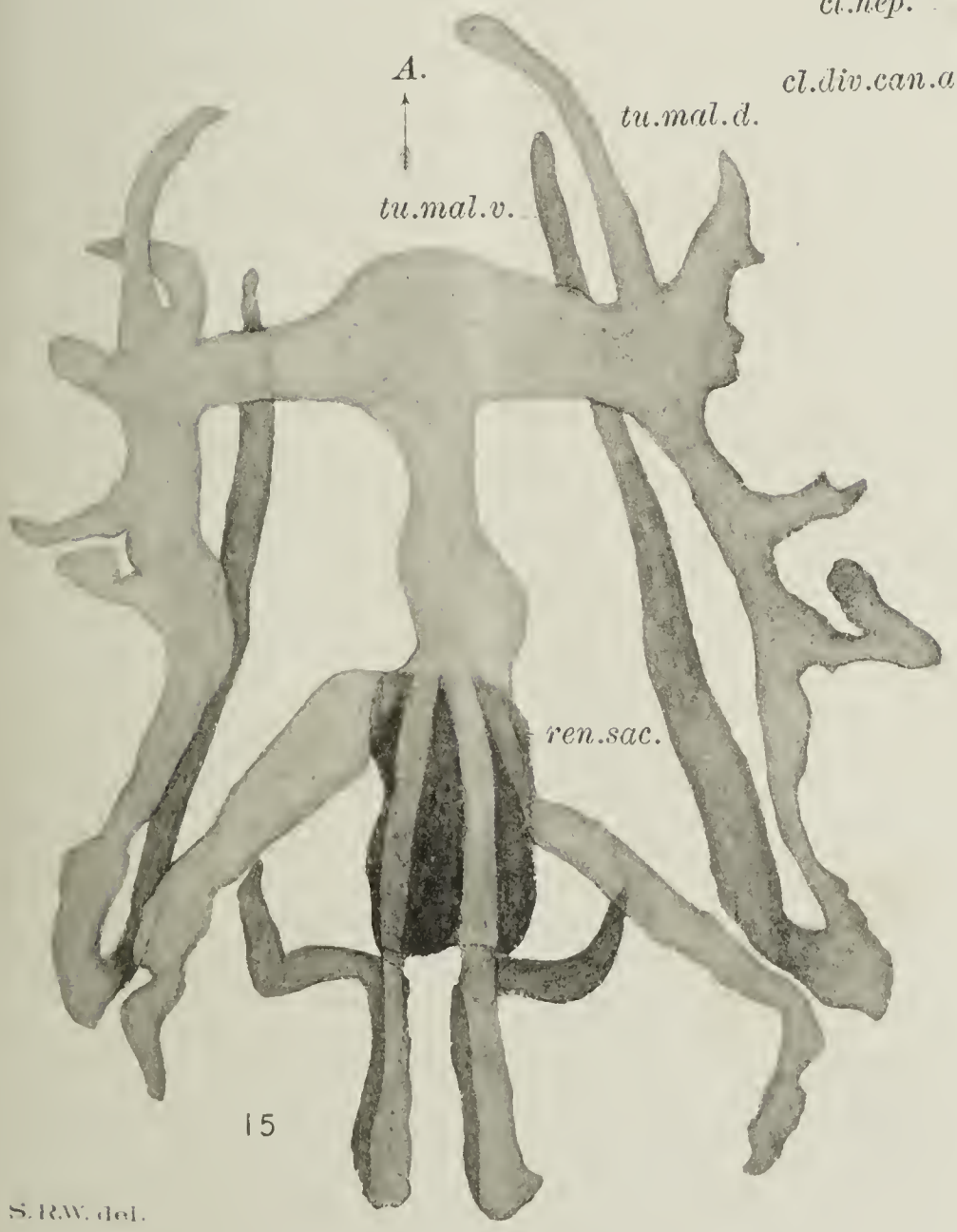

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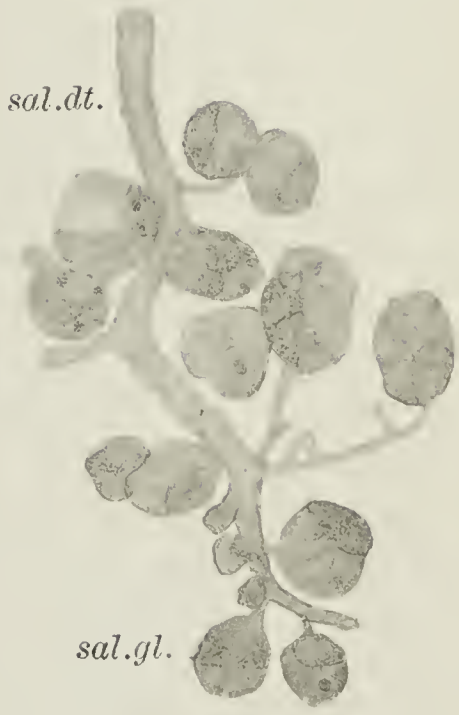

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PLATE 21.

Fig. 16. Cross section showing hypodermis, glands, and adult cuticula; oc. 4 obj. 8 mm., tube 145 mm. × 120.

Fig. 17. Cross section through anterior part of the female reproductive organs; oc. 4, obj. 16 mm., tube 145 mm. × 55.

Fig. 18. Section through the same female 75 μ farther back; oc. 4, obj. 16 mm., tube 145 mm. × 55.

Fig. 19. Dorsal view of ovary of young female; oc. 6, obj. (2 in.). × 25.

Fig. 20. Side view of same ovary; oc. 6, obj. (2 in.). × 25.

Fig. 21. Cross section of ovary of a developing female; oc. 4, obj. 16 mm. × 55.

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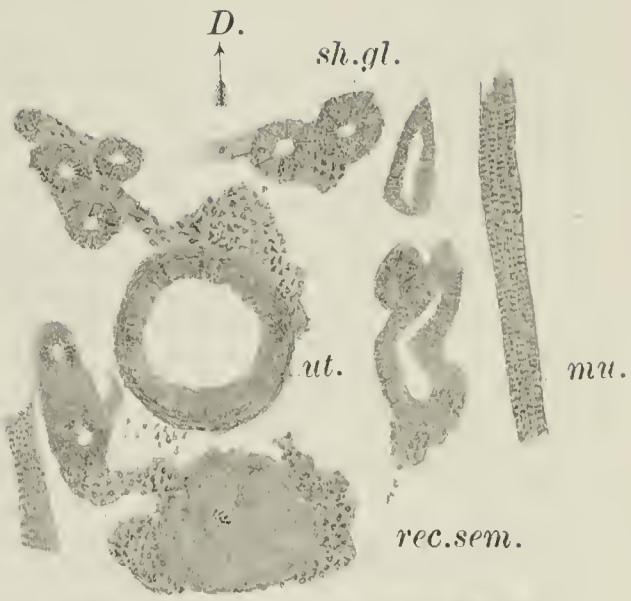

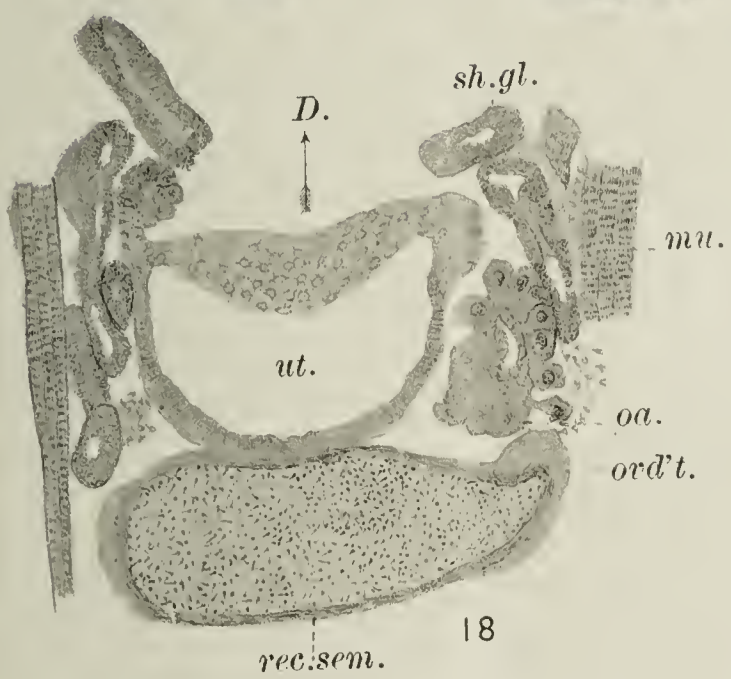

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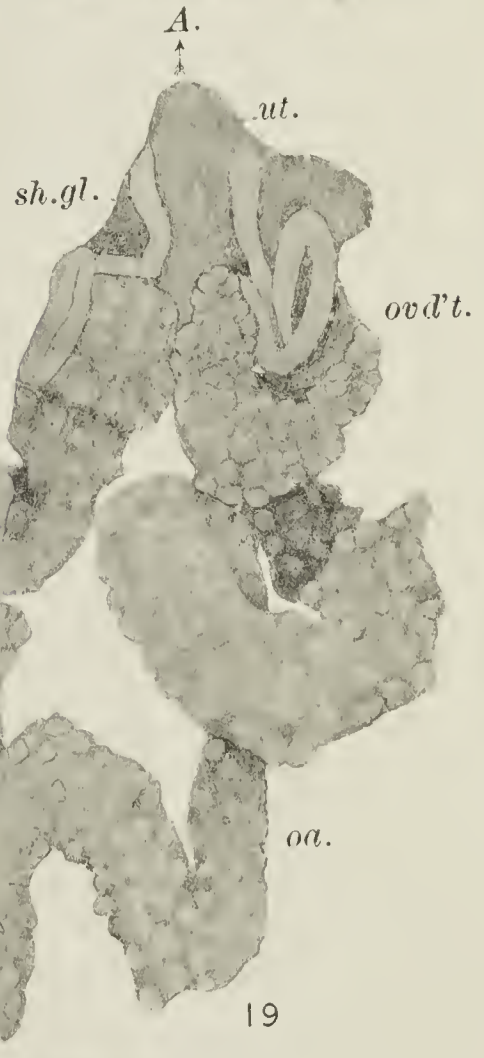

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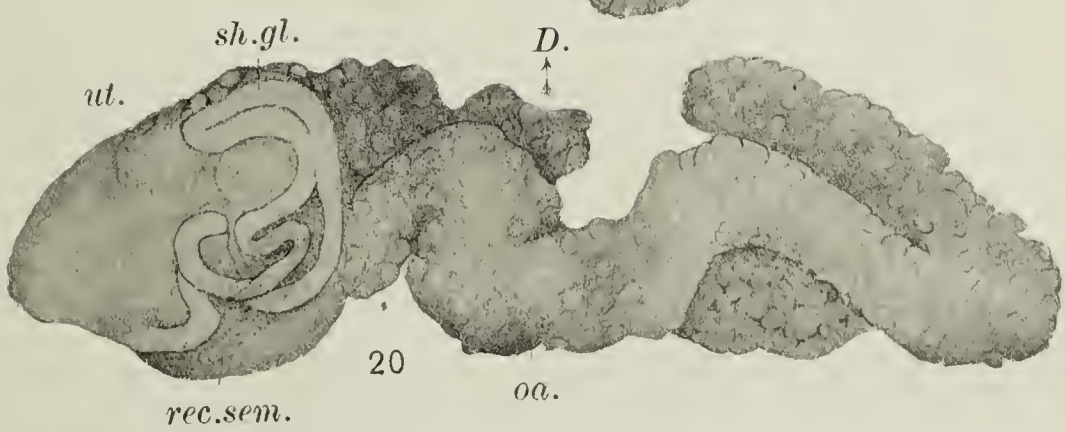

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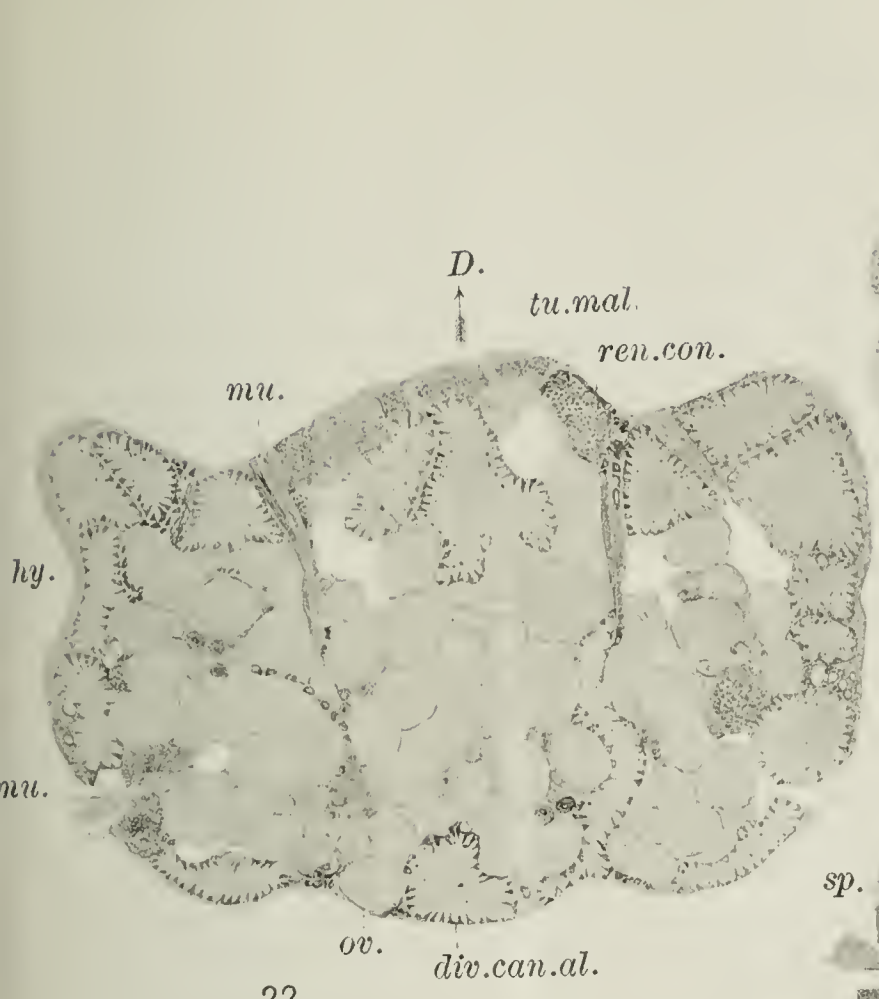
PLATE 22.

Fig. 22. Cross section of gravid female ; dissecting microscope. × 7.5.
Fig. 23. Cross section of seminal vesicles of male ; oc. 4, obj. 8 mm., tube 145 mm. × 120.
Fig. 24. Cross section of testis ; oc. 4, obj. 4 mm., tube 145 mm. × 225.
Fig. 25. Dorsal view of male organs dissected out ; oc. 4, obj. 16 mm., tube 145 mm. × 55.



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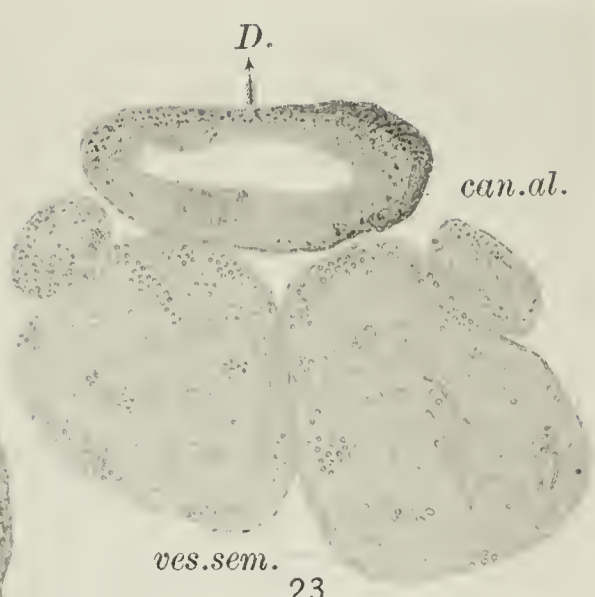

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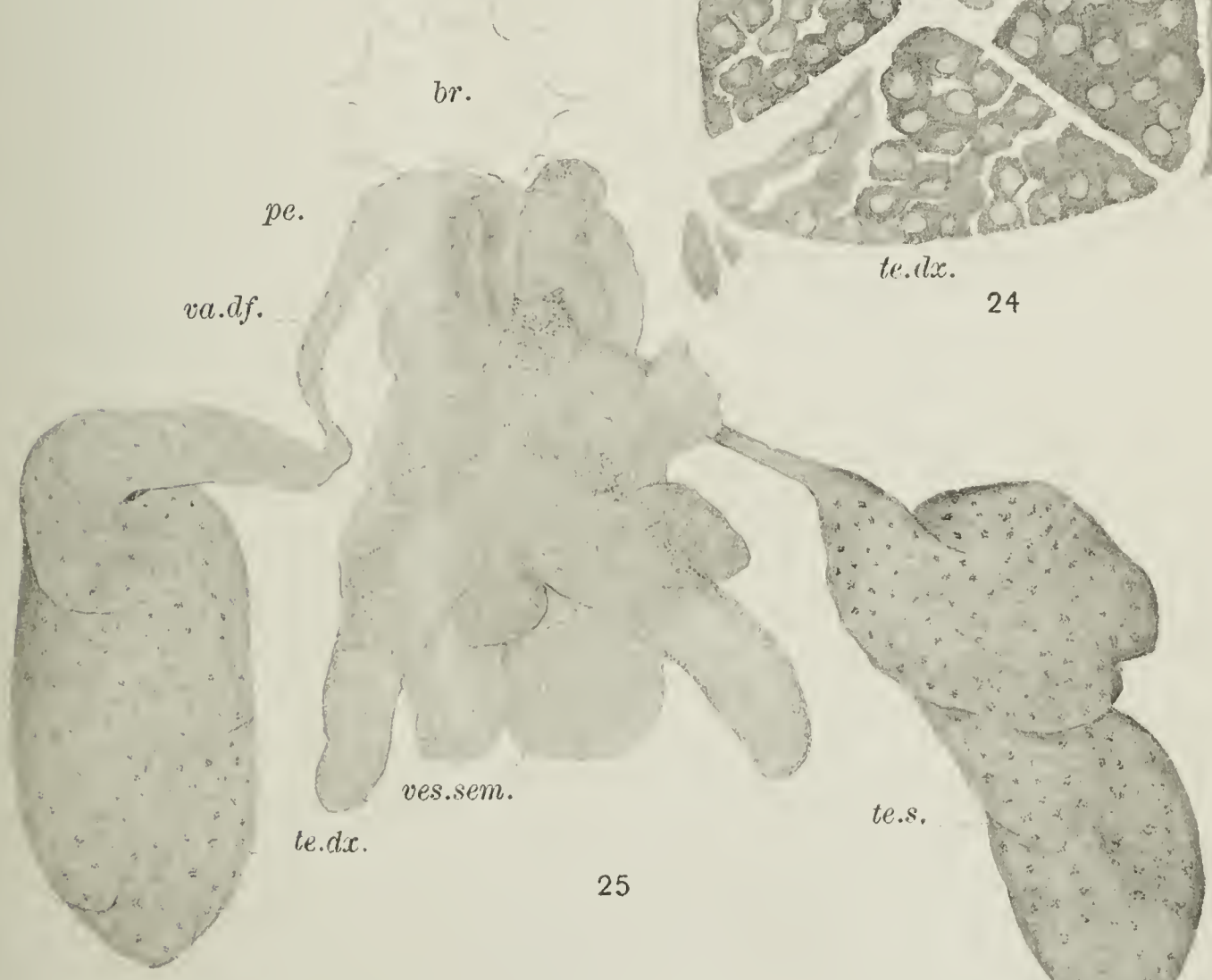

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p. 335–357, pl. 23–26.

CIRCULATORY AND RESPIRATORY SYSTEMS OF *DESMOGNATHUS FUSCA*.

By Anne Barrows Seelye.

BOSTON:

PRINTED FOR THE SOCIETY.

January, 1906.

No. 9.— CIRCULATORY AND RESPIRATORY SYSTEMS OF *DESMOGNATHUS FUSCA*.

BY ANNE BARROWS SEELYE.

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Introduction.

The discovery of lungless salamanders in 1894 by H. H. Wilder, and the physiological investigations by L. Camerano in 1894 and 1896, of two European forms without lungs, suggested an interesting field of study in the integument, considered as an organ of respiration, of one of our native salamanders, *Desmognathus fusca*. As the investigation proceeded, it became evident that the field would have to be widened to include physiological experimentation and a study of the circulatory system. My investigations have therefore been divided into three parts: first, anatomical and histological studies of the integument and its capillary supply; second, physiological experiments to determine the seat of respiration and the permeability of the skin: and third, an anatomical study of the entire circulatory system, including the distribution of capillaries in all regions where respiration seemed possible. Of these three parts the last has received most attention and been most fruitful in results.

The larger part of the work has been carried on in the Zoological laboratory of Smith college, at the suggestion of Prof. H. H. Wilder and with his helpful advice throughout. I am glad of this opportunity to express my gratitude and indebtedness to him. For a half year, in 1897, I pursued these investigations in the Anatomical laboratory of Brown university by the courtesy of Prof. H. C. Bumpus who kindly put at my disposal the abundant resources at his command. It gives me pleasure to acknowledge my gratitude to Professor Bumpus.

The Integument.

Desmognathus fusca has a smooth, slimy skin, attached closely to the muscles beneath it, except in the regions on each side of the neck posterior to the jaws, and under the lower jaw and throat. In these places it is loose and easily removed. The color is dark slate on the

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flanks, brown or slate on the dorsal side, and lighter and semitransparent on the ventral side, where a scattered pigmentation gives it a mottled appearance. An examination of a living specimen with a simple hand lens shows in certain places, especially on and near the legs, a close network of integumental capillaries. These capillaries are found, by a microscopical examination of pieces of skin taken from all parts of the body to be almost evenly distributed over the entire surface of the animal. If a bit of skin be taken from any region of the body, and then dehydrated and cleared in oil of cloves or xylol, the following points are brought out. The thin cuticula is perforated thickly and irregularly with tiny openings (pl. 26, fig. 12, *ex. op.*) which are found to be the openings of flask-shaped slime glands. These openings are of two principal kinds: the commoner form is a simple circular orifice, but there occur also, much less frequently, triangular slit-like openings scattered irregularly over the body surface. Between and around all these glands are black pigment bodies of irregular dendritic shape (pl. 26, fig. 12, *pig.*), varying in their form and arrangement in different individuals, but always more numerous and closer together on the dorsal side of the animal. A curious form of white pigment body, already noted by other investigators in the skin of various other salamanders, is found commonly on the flanks of Desmognathus, among the black bodies.

Partly hidden externally by the pigment, which bears a close relation everywhere to it, is the network of capillaries already mentioned. This can be seen in almost any fresh bit of integument mounted in water and examined under the microscope, but shows much more plainly in the integument of a specimen the circulatory system of which has been well injected with some colored solution (pl. 26, fig. 12, *cap.*). In an injected specimen the largest integumental capillaries measured 28 micra in diameter, the smallest 16 micra.

For the study of the deeper layers of the skin and for its histology, sections of the integument and underlying connective tissue were made at a plane vertical to the surface. Two such sections are shown in plate 26 (figs. 7 and 8). A thin cuticula forms the outermost layer (*cutic.*). This possesses a single layer of flattened nuclei but no cell boundaries. The epidermis (*ep.*), directly beneath this, is formed of three or four irregular cell layers, the nuclei of which are slightly pigmented on their outer sides, the "diffuse pigment" of Gadow. A cutis (*cut.*) about twice as thick as the epidermis underlies it. At the

inner surface of this cutis is found a firm layer, with the appearance in the sections of many fine undulating lines parallel to the surface (*cut. bas.*), which I have called the basement layer of the cutis. Between this and the epidermis, among loose connective tissue and lymph spaces, lie the slime glands (*sl. gl.*), flask-shaped, with long delicate necks or ducts, passing out through the epidermis and cuticula to external openings (*ex. op.*) on the surface. The cuticula lines the outer ends of the ducts. These slime glands are made up of a single layer of cells arranged around a hollow center. Also in the cutis and around and between the glands are found the capillaries (*cap.*) previously observed in a surface view of the skin, and the pigment bodies (*pig.*) already mentioned, lying between and beneath the capillaries. The capillaries are now seen to lie directly underneath the epidermis, sometimes pushing up against its inner boundary so as to make the epidermis slightly thinner in those regions.

A comparative examination was made of the skins of other salamanders: one with rudimentary lungs, *Amblystoma opacum*, and several lunged forms, *Salamandra maculosa*, *Triton alpestris*, *Diemyctylus viridescens*, and *Amblystoma punctatum*. The only point that seemed to hold constant as a difference between the integument of lunged and lungless forms was that the thick layer of wavy-lined appearance on the inner surface of the cutis, basement layer of the cutis (pl. 26, figs. 7 and 8, *cut. bas.*), was much thicker in lungless forms. In some curious way this seems to be correlated with the lungless condition. Beneath the basement layer of the cutis, blood vessels are found in the connective tissue and between the muscles (pl. 26, fig. 7, *cap. sub. cut.*), but these are not nearly as numerous as the subepidermal capillaries.

Physiological Experiments.

An excellent summary of what has been done by previous investigators along the lines of experimentation for determining the respiratory functions of different areas of the amphibian body, is given in the article by Emil Bethge ('98).

The problem which I sought to solve by a series of experiments was as follows. Does *Desmognathus fusca*, or in general do lungless salamanders obtain oxygen and give off carbonic acid gas, first, chiefly by

means of the skin, as was thought to be true in the case of the frog and axolotl by W. F. Edwards and Paul Bert; or, second, almost entirely by means of the anterior portion of the alimentary canal, mouth and pharynx, as Camerano maintained in the case of *Spelerpes fuscus* and *Salamandrina perspicillata*; or, third, by a combination in equal measure of these two methods; or, fourth, by means of the added help of some other part of the body?

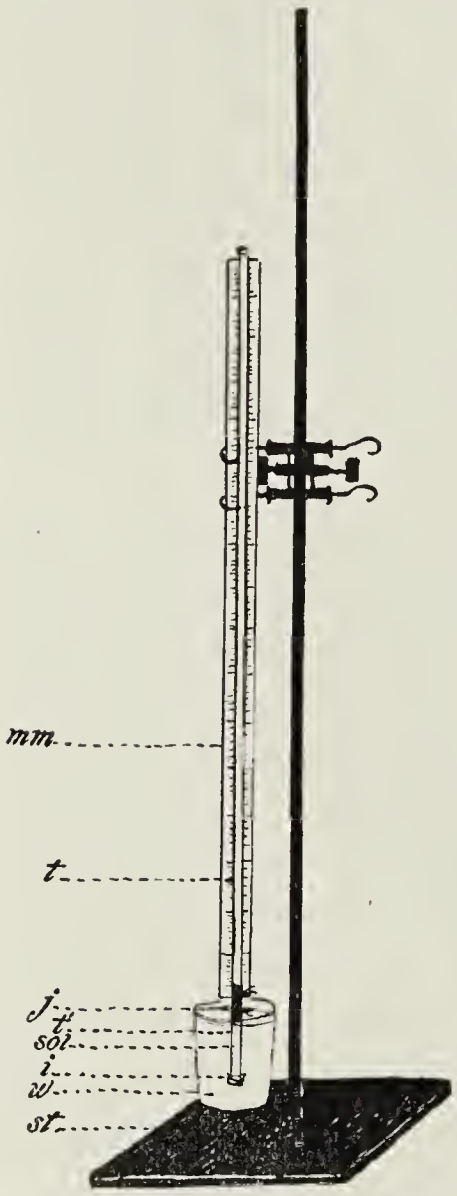

FIG. A.—*mm.*, millimeter scale; *i.*, piece of integument; *j.*, joint made with rubber tubing and wire; *sol.*, sugar solution; *st.*, stand; *t.*, glass tube; *t'.*, shorter glass tube; *w.*, glass tumbler filled with distilled water.

I shall describe the experiments which I devised, dividing them into two groups: first, those made with freshly removed pieces of integument, experiments on the osmotic power of the skin; and second, experiments on the living animal.

In order to test the permeability of the skin of lungless salamanders as compared with the skin of lunged forms, a series of four osmometers was set up as follows. The apparatus is shown in fig. A; to a simple iron chemical stand (*st.*) was attached an upright millimeter scale (*mm.*), with a glass tube (*t.*) firmly wired to it. A shorter glass tube of slightly larger diameter (*t'.*) was then covered at one end by a sufficiently large piece of amphibian integument (*i.*), removed from the underlying connective tissue and muscles of a freshly killed animal. This bit of integument was tied firmly in place by means of a thread. The small tube was then filled with a solution of sugar (*sol.*), water three parts, sugar one part, and jointed firmly to the longer glass tube above by means of rubber tubing and wire (*j.*). The smaller tube was then immersed in a tumbler of distilled water so that the fluids, inside and out, stood at the same level. A bit of thymol, dropped into the water in the tumbler, prevented maceration of the skin during the time that the experiments were set up. The four skins used for these experiments were those of *Desmognathus fusca*, a lungless form;

Amblystoma opacum, a form with rudimentary lungs; *Amblystoma punctatum,* and one of our common frogs, for lunged forms. The results are shown as tabulated records below (p. 340). The apparatus was allowed to remain in each case until the experiment came to a standstill, the liquid in the tube rising at first and then falling as the fluids inside and out became mixed through the integument, or until the experiment was interrupted for other reasons.

The conclusion to be drawn from these experiments seems to be that the skins of the lunged forms are more easily and quickly permeated by the liquid than those of the lungless forms. However, it is immediately seen that a larger number of such experiments is needed upon which to base any very sound conclusions.

The problem in hand, moreover, was not how liquids could permeate the skin, but whether an exchange of gases could take place there. A more pertinent experiment was made by means of an apparatus shown in fig. B. Carbonic acid gas was used, with lime-water to test its presence. Four small vials (*v.*) were filled with lime-water, and over the tops were firmly tied pieces of integument (*i.*, 1, 2, 3, and 4), removed from four different amphibians, two lungless and two lunged forms. The animals used were *Desmognathus fusca,* lungless; *Spelerpes bilineatus,* lungless; *Amblystoma opacum,* lungs rudimentary; and *Diemyctylus viridescens,* lungs fully developed. These four vials were then inserted in a cork disk (*c.*) to hold them upright, and this carefully placed in a large-mouthed glass bottle. The large bottle was then filled with carbonic acid gas and tightly closed with a rubber stopper. The apparatus thus set up was allowed to stand while the lime-water was carefully watched to see when it first became milky, a sign of the presence of CO_2, and when it again became clear, a sign of excess of CO_2. The results are tabulated below (p. 341):—

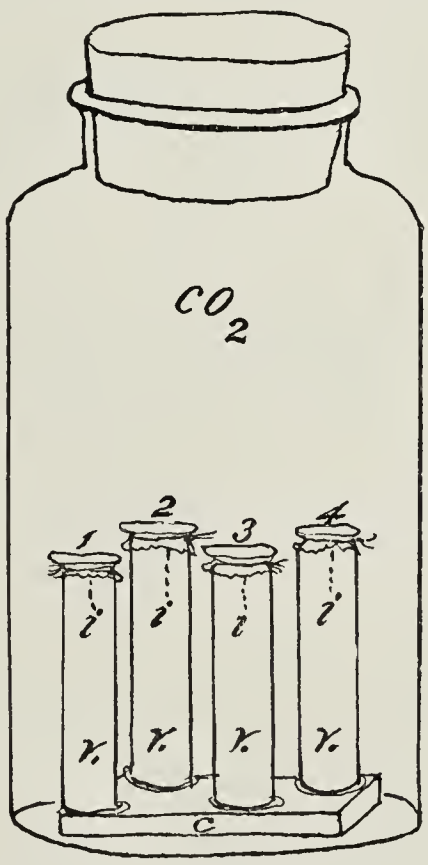

FIG. B.— *c.*, cork disk; *i.*, integument: (1) of *Amblystoma opacum,* (2) *Desmognathus fusca,* (3) *Spelerpes bilineatus,* (4) *Diemyctylus viridescens*; *v.*, small vial filled with lime water.

From this experiment we may conclude that gases can permeate

Desmognathus fusca				*Amblystoma opacum*				*Amblystoma punctatum*				*Frog*			
Date	Time		Height of fluid in tube	Date	Time		Height of fluid in tube	Date	Time		Height of fluid in tube	Date	Time		Height of fluid in tube
			cm.				cm.				cm.				cm.
Nov. 20	4	P. M.	0.0	Dec. 18	3	P. M.	0.0	Dec. 4	4	P. M.	0.1	Nov. 27	11	A. M.	0.0
" "	5	P. M.	0.2	" 19	9.30	A. M.	10.5	" "	5	P. M.	0.6	" "	2	P. M.	0.75
" 21	8	A. M.	3.6	" 20	10	A. M.	22.5	" "	6	P. M.	1.4	" "	4	P. M.	1.4
" "	12	M.	4.1	" 21	10	A. M.	29.3	" 5	8.30	A. M.	12.0	" "	6	P. M.	2.3
" "	6	P. M.	4.7	" 23			31.0	" "	12	M.	14.5	" 28	8	A. M.	6.7
" 22	10	A. M.	5.3					" "	3 30	P. M.	16.8	" "	11	A. M.	7.4
" "	3	P. M.	5.2					" 6	1	P. M.	28.9	" "	1	P. M.	7.6
" "	5	P. M.	5.1					" 7	2	P. M.	38.7	" "	6	P. M.	8.0
" 23	8.30	A. M.	4.6					" 8	11	A. M.	44.8	" 29	10	A. M.	7.6
" "	2.30	P. M.	4.4					" 9	11	A. M.	50.0	" "	6	P. M.	7.0
" "	8	P. M.	4.0					" 10	11	A. M.	53.8	" 30	8.30	A. M.	6.1
" 24	11	A. M.	3.0					" 11	11	A. M.	56.5	Dec. 1	8	A. M.	4.6
" "	4.30	P. M.	2.6					" 12	9	A. M.	58.4	" 2	1	P. M.	2.9
" 25	8.30	A. M.	1.5					" 13	9.30	A. M.	60.0	" 3	9	A. M.	2.0
" "	4.30	P. M.	1.1					" 14	7	P. M.	60.8	" "	5	P. M.	1.5
" 26	9	A. M.	1.3									" 4	9	A. M.	1.0
" 27	9.45	A. M.	1.2									" "	12	M.	0.9
" "	11.30	A. M.	1.4									" "	3	P. M.	0.8
" "	2	P. M.	1.5									" "	4	P. M.	0.7
" "	4	P. M.	1.7									" "	5	P. M.	0.6
" "	6	P. M.	1.8									" 5	8.30	A. M.	0.1
" 28	8	A. M.	1.7									" "	12	M.	0.1
" "	11	A. M.	1.6									" "	3.30	P. M.	0.3
" "	1	P. M.	1.5												
" "	6	P. M.	1.2												
" 29	10	A. M.	0.7												
" "	6	P. M.	0.5												
" 30	8.30	A. M.	0.1												
Dec. 1	8	A. M.	0.0												

urodele integuments. It also seems to show that the skins of lunged forms, *e. g.*, Diemyctylus, are more quickly and easily permeated by a gas than are those of the lungless animals. The skin of *Amblystoma opacum*, the intermediate form with rudimentary lungs, was slowest in first allowing the gas to pass through, but the excess of CO_2 showed more quickly here than in the case of the lungless forms. Of course it must be remembered that, as we saw in our anatomical study of the integument, the majority of the blood vessels are intra- and not sub-integumental, so that normally a gas would not have to pass through the basement layer of the cutis as it did in the experiment.

Time	*D. fusca*	*S. bilineatus*	*A. opacum*	*D. viridescens*
2 P. M.	clear	clear	clear	clear
2.40 P. M.		milky streaks		milky streaks
2.55 P. M.	milky streaks			
3.45 P. M.		more milky	milky streaks	more milky
5 P. M.	evenly milky	evenly milky	evenly milky	evenly milky
10 P. M.	very milky	very milky	clear	clear
6 A. M.	clear	clear	clear	clear

The second group of experiments dealt with the living animals, and included a series of tests of the effect of chloroform taken into the mouth, pharynx, and esophagus, as compared with its effect on the skin. Here again lungless and lunged forms were used. *Desmognathus fusca* was the animal experimented upon, and *Diemyctylus viridescens* the control animal.

The first of these tests, for the effect of chloroform taken in at the mouth, was set up as shown in fig. C.

A glass tube (*g. t.*), open at both ends and large enough to receive the head of a salamander, was employed as a chloroform chamber. Strong pieces of thread were tied around the fore legs of the animal, and these were fastened to the end of the glass tube through small holes (*h.*), previously burned in the glass, so that the animal's head was firmly held inside the tube. A strip of absorbent cotton soaked in water (*c'.*) was then placed at the joint to make it as nearly tight as possible. Chloroform on an absorbent cotton wad (*c.*) was then introduced into the tube and the end opposite the animal's head closed with a rubber stopper (*s.*). In order to maintain as normal a condition as possible for the parts exposed to the air, a damp towel was placed under the animal's body, and the skin kept moist and cool during the

experiment by means of water from a pipette and by fanning. Both Desmognathus and Diemyctylus, under conditions as nearly as possible alike, were left for a half hour in this position.

When first removed from the tube, the lungless form, Desmognathus, was much more lively than Diemyctylus. It moved around in an active manner on the table, and swam when put into water, turning over with quick motions. The lunged form, Diemyctylus, made no voluntary movements on the table nor in water. Both forms responded to mechanical stimuli and to the stimulus of drops of acetic acid applied to various parts of the body. They were placed in the terrarium, from which they had been taken, in order to secure a return to conditions as normal as possible. Desmognathus did not cease to

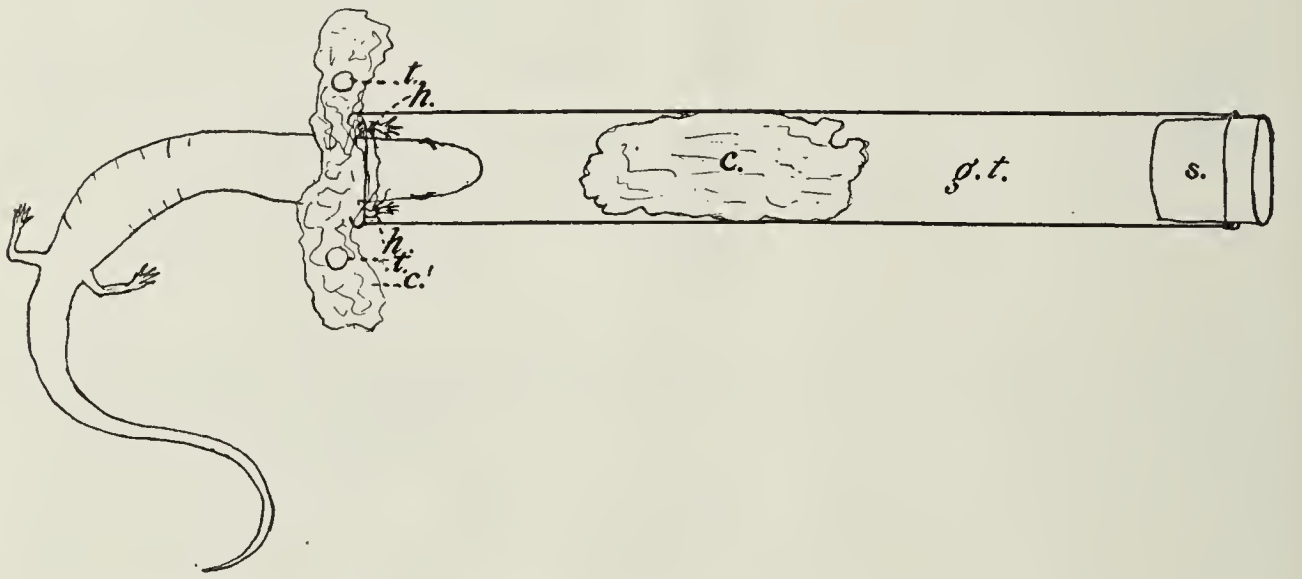

FIG. C.— *c.*, wad of absorbent cotton soaked in chloroform; *c'.*, strip of absorbent cotton soaked in water; *g.t.*, glass tube; *h.*, hole in glass tube for thread; *s.*, rubber stopper; *t.*, tack.

respond to stimuli for almost forty-three hours, after which it died. Diemyctylus responded to stimuli for a much shorter time, about twenty-six hours, before all signs of life failed.

The second set of tests on the living animal was made to bring about conditions opposite to those just described. The supply of air to the mouth was free and the influence of chloroform was brought to bear on as much of the surface of the skin as possible. Here again *Desmognathus fusca* and *Diemyctylus viridescens* were used for experimentation. The apparatus is shown in fig. D. A rubber stopper (*p. s.*) was perforated with a hole large enough to receive the salamander's head and fore limbs. The head protruded from the outer end of the stopper, and the fore limbs were fastened there by means of thread

(*th.*) tied through small holes in the rubber stopper. Another smaller perforation through the stopper received the end of a thistle tube (*tt.*). The stopper, with the animal thus attached, was then placed in the mouth of a glass bottle (*b.*) so that the head was outside and the body within the bottle. To make the joint tight around the animal's neck, and yet not constrict the neck, a piece of thin rubber tissue (*r.*) with two small perforations in it was stretched over the animal's head and over the thistle tube, and tied tightly around the neck of the bottle, leaving the head and thistle tube outside as shown in fig. D. The bottle was then placed on its side with the animal's dorsal side uppermost, and chloroform was introduced through the thistle tube which was afterwards closed by a stopper (*s.*). A piece

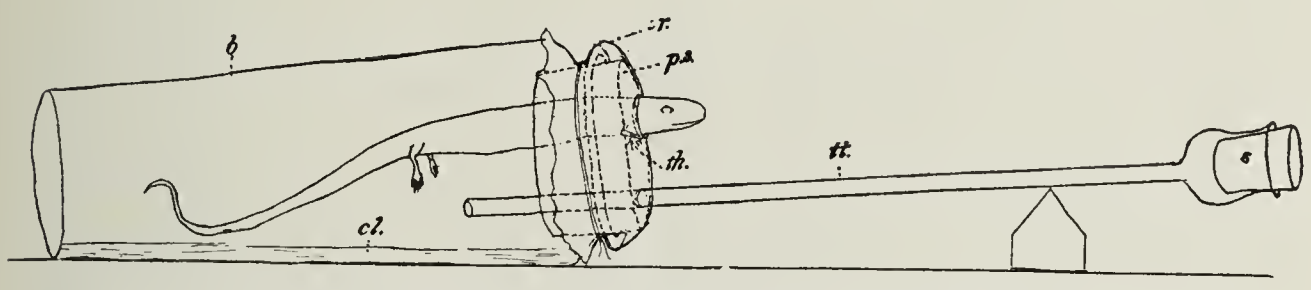

FIG. D.—*b.*, bottle; *cl.*, chloroform; *ps.*, perforated rubber stopper; *r.*, rubber tissue; *s.*, stopper; *th.*, thread tying in leg; *tt.*, thistle tube.

of absorbent cotton soaked in water was placed around the animal's neck to prevent the escape of any fumes of chloroform at that place. Each animal was left for half an hour subject to this experiment. The head was constantly moistened and air fanned to it. The results were as follows. In the case of *Desmognathus fusca* the body moved in a lively manner at first, then became stiff and rigid and white with exuded slime. The head, however, responded to mechanical stimulation, and when the animal was released at the end of the half hour, although the body was rigid, the mouth was voluntarily opened wide repeatedly. The animal was put into the terrarium but died in two and a half hours. In the case of *Diemyctylus viridescens*, the lunged form, there were active breathing movements all the time that the experiment was going on. The mouth opened and shut with a snapping noise, and when the animal was released it moved its head voluntarily. It was put back in the terrarium and died in five and a half hours.

These results seem to show that the skin plays an important part in the respiration of both lunged and lungless forms, but that it is a rela-

tively smaller part in the case of the animals with lungs. In other words the lungs perform more of the respiratory function in the lunged forms than do the bucco-pharyngo-esophageal parts in the lungless forms, although the function of the latter parts is shown to be an important one.

In general the few conclusions that can be drawn from these interesting but necessarily imperfect and limited experiments on the osmotic function of the skin and on the respiratory activities of the animals themselves, are that contrary to Camerano and in accordance with Bethge's view, cutaneous respiration plays an important part in the life of lungless salamanders, and that the respiration carried on in mouth, pharynx, and esophagus must also be of high importance.

The Circulatory System.

When my dissections and drawings of the circulatory system of Desmognathus were nearly completed, Emil Bethge published, in 1898, an article entitled "Das blutgefässsystem von *Salamandra maculata, Triton taeniatus,* und *Spelerpes fuscus;* mit betrachtungen über den ort der athmung beim lungenlosen *Spelerpes fuscus.*" This work included, besides a study of the anatomy of the main blood vessels of these animals, an account of the distribution of the capillaries in the skin, pharynx, and esophagus. It therefore covered some of the ground that I had been investigating, but the lungless form which Bethge studied for the purpose was a different one. *Spelerpes fuscus* is a much larger salamander than Desmognathus, but Bethge did not try to work out in detail the course of as many veins and arteries as I have done in the case of Desmognathus. The comparison with his work thus afforded was, however, extremely interesting and of great service to me.

The following is a recapitulation of the important peculiar points in the circulatory system of *Spelerpes fuscus* as worked out by Bethge:—

1. The total absence of a vena pulmonalis.
2. An arteria maxillaris externa arising from the second arterial arch on each side and branching to upper and lower jaw.
3. An arteria occipitalis branching into the tissue of the roof of the mouth and sending one branch to the eye.
4. Two arteriae vertebrales collaterales, communicating with the

aorta and giving off at each vertebra a ramus dorsalis and a ramus costalis with extremities terminating in the skin.

5. A small arteria cutanea magna branching from a. subclavia.

6. An arteria pulmonalis, really the fourth arterial arch, sending one branch to the skin and passing along the lateral surface of the stomach to anastomose with the a. gastrica.

7. A large vena cutanea magna, with a branch, vena cutanea parva, opening into the ductus Cuvieri.

8. A vena subclavia opening separately into the ductus Cuvieri.

9. A vena oesophagea.

10. Two venae caudales instead of one.

11. An arteria pharyngea.

The capillary distribution in Spelerpes, as worked out by Bethge, may be summed up as follows: in the skin the capillaries are directly beneath the epidermis, they surround the glands all over the body, and are accompanied by pigment. The width of these cutaneous capillaries was from 24 to 30 micra in Spelerpes, while in Triton they measured from 12 to 16 micra, and in Salamandra only from 7 to 12 micra. In the esophagus Bethge speaks of a rich network of blood vessels, and shows drawings of sections through the esophageal wall in which the capillaries lie among the epithelial cells, while in stomach and intestine they reach only to the epithelium. In Salamandra the network is especially rich in the region of the glottis, and in Spelerpes there is an area rich in capillaries where a glottis may once have been. The capillaries of the pharynx and mouth of Spelerpes are described by Bethge as bearing little swellings or diverticula so that they look almost like stems with berries on them. He refers to a similar appearance noted by Langer in 1867 in the frog.

Bethge makes these general conclusions from his studies of the distribution of blood vessels in Spelerpes: that cutaneous respiration must be very important in lungless salamanders; that although the capillaries are nearer the surface in mouth, pharynx, and esophagus and are diverticulated, still the much greater extent of the skin capillaries equalizes this, if it does not overbalance it; that the fact that some tissues take a large amount of their oxygen directly and solely from blood coming from the skin speaks for the importance of cutaneous respiration; and that Camerano's statement that cutaneous respiration is unimportant in the case of *Spelerpes fuscus* must be contradicted; both kinds of respiration are necessary to the life of this animal.

I shall describe briefly the principal blood vessels that I have found in *Desmognathus fusca,* and their distribution, as well as the capillary conditions in this lungless form. Both the larger and smaller vessels differ in certain points from those of Spelerpes. The operation of injecting so small an animal was exceedingly difficult and only after repeated failures was success attained. A warm carmine-gelatin mass was used, with a freshly killed specimen, the body of which was constantly bathed in warm water. For forcing the fluid into the heart, a small hypodermic syringe was employed, with the point of the needle filed down blunt, and a groove filed near the end to keep the ligature from slipping. This blunt end of the needle was introduced through the snipped-off tip of the ventricle and tied in place. The accompanying figures (pls. 23–25, figs. 1–6) show the parts enlarged to five times their natural size, except fig. 4 (pl. 24) which is about ten times natural size. It was impossible to include all the blood vessels in one drawing with any clearness, and therefore the six drawings are intended to supplement one another. The colors are to indicate anatomical distinctions, blue for veins and capillaries, red for arteries.

Beginning with the venous system, which is the one most superficial on opening the animal from the ventral side (pl. 23, figs. 1, 2), we find the blood from the anterior region of the body brought to the sinus venosus through the ductus Cuvieri by a large vein, the vena jugularis interna. In pl. 25 (fig. 5) is shown the origin of this vein, formed by the union of the venae maxillares, superioris and inferioris. The vena maxillaris inferioris is shown in pl. 23 (fig. 1). It starts at the tip of the jaw from an anastomosis with the vein of the opposite side, and follows the course of the lower jaw. The vein of the left side in many specimens studied, but not in all, received a large branch near the anterior end of the jaw, that arose in a peculiar bunch of little white tubules near the base of the tongue. The vena maxillaris superioris is made up of branches from each side of the eyeball (pl. 25, fig. 5).

Opening into the ductus Cuvieri at the same point as the vena jugularis interna is the large vena cutanea magna (pl. 23, fig. 1). This receives on its course branches from the sides of the animal (pl. 25, fig. 5), and one relatively large branch from the skin of the dorso-lateral part of the head, that seems to correspond to Bethge's vena cutanea parva (pl. 25, fig. 6).

The vena jugularis externa is a small branch made up of the vena

lingualis and a side branch, and passes through the "rete mirabile" of Bethge, to open into the vena cutanea magna (pl. 23, fig. 1). Near this opening and toward the median line another small vein, the vena pharyngea (pl. 23, fig. 1), opens into the vena eutanea magna.

The remainder of the blood from the posterior regions of the body is brought to the sinus venosus by means of the vena abdominalis, vena porta hepatis, vena eava posterioris, and vena hepatica revehens. We shall traee the course of eaeh of these veins separately.

The vena abdominalis differs from any described by other investigators in being formed not by braneheS from the venae iliacae on each side, but by two branches, rami abdominales (pl. 23, fig. 1), from the venae iliacae eommunes as they pass along the latero-dorsal sides of the kidneys, and by braneheS from the bladder (vena vesicularis), the reetum (vena haemorrhoidalis), and the ventral body wall (venae musculares) (pl. 23, fig. 1).

The vena abdominalis empties into the vena porta hepatis, which also receives branches from the intestine (vena intestinalis), the mesentery (vena mesenterica), the spleen (vena lienalis), the stomaeh (venae gastricae), the stomaeh and duodenum (vena gastrieo-duodenalis), and the esophagus (venae oesophageae) (pl. 23, figs. 1, 2; pl. 24, figs. 3, 4). These esophageal veins seem to eorrespond to those found by Bethge in Spelerpes.

The venae iliaeae eommunes, receiving blood from the tail, venae caudales, and from the hind limbs, venae iliacae, send part of their blood through the rami abdominales, and part through the venae renales advehentes to the kidneys (pl. 23, fig. 1).

The vena cava posterioris arises by braneheS, venae renales revehentes, from between the kidneys (pl. 24, fig. 3), passes anteriorly, receiving a few branches from the genital organs and from the reetum, traverses the right dorsal portion of the liver (pl. 23, fig. 2), receiving a few braneheS from the liver, and opens with the vena hepatica revehens, from the ventral side of the liver, into the sinus venosus (pl. 23, fig. 1).

The venae eaudales, two in number as in Spelerpes, with a cross connection posterior to the kidneys, the venae iliaeae from the posterior limbs, and the venae subclaviae remain to be mentioned. These are all shown in plate 23 (fig. 1). A eurious instanee of the one-sidedness of this circulatory system is seen in the case of the venae subelaviae, whieh instead of opening at opposite sides into the sinus

venosus, open into it together on the left side. In order to accomplish this, the vein from the right fore limb makes a curve around the ventricle of the heart (pl. 23, fig. 1). This seems to be a constant feature, and fits in with the movement of the sinus venosus to the left side, first described by Hopkins, in 1896.

The arterial system may be traced from the truncus arteriosus where three arches arise on each side instead of four (pl. 23, fig. 1; pl. 24, fig. 3; pl. 25, fig. 5). My results on this point coincide with those of Bethge in the case of Spelerpes.

The first arterial arch gives rise to the arteria carotis, which sends off on the ventral side an arteria carotis externa, and then continues around the esophagus to the dorsal side as arteria carotis interna, and thence into the skull to the brain (pl. 24, fig. 3; pl. 25, fig. 5).

The second arch forms the aorta, but first gives off three branches on each side: an arteria occipitalis, an arteria maxillaris externa, and an arteria vertebralis collateralis (pl. 25, fig. 5).

The occipital artery arises on the dorsal side and courses anteriorly near the inner margin of the eyeball (pl. 25, fig. 5).

The external maxillary artery branches off from the second arch on each side, nearer the lateral region, passes outward and forward, giving off a branch to the dorsal wall of the esophagus and pharynx (pl. 24, fig. 4), and then divides to send one branch to the lower and one to the upper jaw (pl. 23, fig. 1).

The arteria vertebralis collateralis arises from the dorsal side, nearer the median line than the external maxillary (pl. 25, fig. 5). It sends a branch to the skin at the side of the neck, and then passes posteriorly close to the vertebral column. It sends branches at each vertebra to the muscles of the dorsal and ventral body wall and skin. The two arteriae vertebrales collaterales communicate by means of nine or ten branches, between fore and hind limb regions, with the aorta. The first one or two of these branches pass from the aorta in an anterior instead of a posterior direction (pl. 25, fig. 5), a curious fact that was noted by Bethge in Spelerpes. It would seem to hinder the flow of blood from the aorta, unless the blood might flow in those branches from the arteriae vertebrales collaterales to the aorta.

The two radices aortae unite to form the aorta at a point dorsal to the ventricle of the heart. The aorta in its posterior course gives off the following vessels: two arteriae subclaviae (pl. 23, fig. 1; pl. 24, fig. 3; pl. 25, fig. 5), each of which in turn gives off posteriorly an arteria sternalis (pl. 23, fig. 1); four arteriae gastricae (pl. 24, figs. 3,

4; pl. 25, fig. 5), very near the arteriae subclaviae and arranged asymmetrically; several arteriae genitales on each side (pl. 24, fig. 3); an arteria intestinalis communis (pl. 24, fig. 3; pl. 25, fig. 5); groups of arteriae mesentericae and arteriae urogenitales (pl. 24, fig. 3); two arteriae epigastricae (pl. 23, fig. 1; pl. 24, fig. 3; pl. 25, fig. 5); two arteriae iliacae (pl. 23, fig. 1; pl. 24, fig. 3; pl. 25, fig. 5); and two small branches to the cloacal glands (pl. 23, fig. 1; pl. 24, fig. 3).

Several of these aortic branches require particular description. I have mentioned the fact that the four gastric arteries are disposed asymmetrically. The usual arrangement is one on the right side and three on the left side. The two anterior gastric arteries, one on each side, turn anteriorly and anastomose with the arteriae pulmonales, right and left. This anastomosis is shown on the right side in plate 24 (fig. 3) and will be spoken of again in connection with the arteria pulmonalis. The anastomosis was broken in removing the portion of the alimentary canal shown in plate 24 (fig. 4) and so cannot be seen in that drawing.

The arteria intestinalis communis and its branches are best shown in plate 24 (fig. 3). The branches are: an arteria hepatica, supplying the liver; an arteria lienalis, distributing to the spleen; an arteria duodenalis, which traverses the pancreas and distributes to the posterior end of the stomach and to the duodenum; and an arteria mesenterica anterioris, supplying the anterior region of the mesentery and intestine.

The artery on each side of the aorta anterior to the iliac artery, which I have called arteria epigastrica, from its resemblance to that vessel in other animals, is a comparatively large and important branch of the aorta in Desmognathus, and was not mentioned by Bethge as occurring in Spelerpes. It turns anteriorly and courses along the ventrolateral body wall. Its distribution is best shown in plate 23 (fig. 1) and its aortic origin in plates 24 and 25.

There remains for consideration the third of the existing arterial arches, morphologically the fourth arch, as previous investigators have demonstrated. In lunged forms this supplies lungs and skin, and therefore its occurrence in lungless forms is of especial interest. In Desmognathus I find a condition which agrees with that found by Miss Woldt in Plethodon and by Bethge in Spelerpes, although I differ from the latter in the naming of one of the branches. The arteria pulmonalis (pl. 24, fig. 3) is well developed in Desmognathus, although of course much smaller than the other two arches. It sends off an

arteria pharyngea (pl. 24, figs. 3, 4) to the ventral wall of pharynx and esophagus, and also sends out a small branch laterally, which seems to me from its origin and distribution to be a small arteria cutanea (pl. 24, fig. 3). The pulmonary artery then passes posteriorly along the esophagus and stomach, and anastomoses with a branch of one of the gastric arteries, as previously stated.

The foregoing description covers the anatomy of the main blood vessels in Desmognathus. A curious condition in this animal, which seems to call for more particular discussion, is the nomenclature and relation of the two arteries which I have called arteria sternalis and arteria epigastrica. The former is the same vessel which Bethge calls arteria cutanea magna. As this name is given in most other Amphibia to the artery which branches from the pulmonary arch and supplies a portion of the skin, it has seemed to me more fitting to keep the name arteria cutanea for the small branch already mentioned, which in Desmognathus arises from the pulmonary arch and supplies the skin of the side of the neck (pl. 24, fig. 3). The branch from the subclavian artery (pl. 23, fig. 1, *a. ster.*), Bethge's arteria cutanea magna, moreover, bears a close resemblance to what is named arteria sternalis in mammals, arteria thoracico-abdominalis in the frog (Gaupp). A similar branch of the subclavian in Triton and Salamandra was shown by Bethge to course over the ventral wall of the trunk and anastomose with the superficial epigastric artery. I have called the branch of the aorta anterior to the iliac artery, arteria epigastrica (pl. 23, fig. 1; pl. 24, fig. 3), although it has here an independent origin from the aorta. It is possible that we have in Desmognathus an indication of a condition more primitive than that in mammals,— a series of segmentally arranged vertebral arteries, which were once all connected by anastomoses, and that later in vertebrate development the connections with the aorta of the middle part of the series were lost, and the anastomoses made one continuous artery along the ventral wall of the trunk, the arteria sternalis of mammals.

In summary, I have noted the following differences between the disposition of blood vessels in Desmognathus and that in Spelerpes as shown by Bethge:—

1. The vena subclavia entering the sinus venosus directly, instead of first opening into the ductus Cuvieri; and the right and left venae subclaviae opening together into the sinus on its left side.

2. The vena abdominalis arising, not from the venae iliacae, but from the venae iliacae communes.

3. A side tributary of the vena lingualis, observed, however, only on the left side.

4. The arteria cutanea, a branch of the arteria pulmonalis, instead of a branch of the arteria subclavia.

5. Four arteriae gastricae at anterior end of stomach, instead of two; three of these go to one side (the left).

6. The presence of the arteria epigastrica, an important branch from the aorta just anterior to the arteria iliaca.

We have next to consider the capillary distribution in mouth, pharynx, and esophagus. The integumental capillaries have already been described in the section on the skin. While my investigations were in progress an article appeared, by F. Maurer ('97), entitled "Blutgefässe im epithel." Maurer showed the presence of capillaries in the epithelium itself of the mouth cavity of a frog. Following the technique which he outlined, I made sections through the buccal epithelium of Desmognathus, and succeeded in showing capillaries even nearer to the surface than Maurer had done. These sections are shown in plate 26 (figs. 9, 10); *sup.* indicates the superficial surface, and the nearness of the capillaries (*cap.*) to it is remarkable. The pharyngeal capillaries measured from 4 to 28 micra in diameter, but the results of these capillary measurements and those of Bethge seem to me untrustworthy because they were taken on injected blood vessels, and the diameter of a capillary might vary with the amount of injecting fluid forced into it. A study of a bit of injected pharyngeal epithelium, dehydrated and cleared, revealed curling and twisting capillaries in a close network, as shown in plate 26 (fig. 13), but no diverticula nor marked swellings such as Bethge described and pictured for Spelerpes. An appearance of a diverticulum or swelling, shown in the drawing of the outline of the capillaries, always proved, by focusing up and down on the object, to be a bend in the capillary as it passed in a plane at right angles to the slide (pl. 26, fig. 13, places marked *b*).

A careful study of the esophageal region in a well injected specimen brought to light a marvelously fine and extensive network of capillaries on the esophagus. Branches of the arteria maxillaris externa on the dorsal side, and of the arteria pharyngea on the ventral wall, become finely subdivided as shown in plate 24 (fig. 4). From these capillaries the blood is taken up by the veins, especially the esophageal vein with its tributaries. Further details of these esophageal capillaries are

given in my preliminary paper, "The respiration of Desmognathus," (Barrows, :00).

The question as to whether these capillaries extend into the epithelium of the wall was answered by sectioning a portion of the esophagus in this region. Examination of these sections showed the capillaries well within the epithelium (pl. 26, fig. 11) just as Bethge showed them in Spelerpes and Salamandra.

General Conclusions.

From these studies of the integument, from the physiological experiments, and from the investigations on the anatomy of the circulatory system, macroscopic and microscopic, we may then draw certain general conclusions:—

Desmognathus is furnished with an important breathing organ in the anterior portion of the alimentary canal, mouth, pharynx, and esophagus. An article by H. H. Wilder (:01) entitled "The pharyngo-esophageal lung of Desmognathus," appeared while I was completing my studies of the circulatory system. From the results of some of my work and from his own study of the respiratory muscles Dr. Wilder has maintained that functionally this pharyngo-esophageal region takes the place of a lung.

It seems to me, however, that the skin also plays an important part in the respiration of this animal, as was indicated by my experimental tests, as well as by the extensive distribution of cutaneous blood vessels, and the subepidermal network of capillaries very evenly distributed over the entire body. The integumental region around the sides of the neck, where the skin is free from the underlying muscles, seemed to be especially richly supplied with subcutaneous blood vessels. Here the arteria cutanea from the pulmonary arch, and a branch of the arteria vertebralis collateralis, on each side, bring blood to the skin; while the vena cutanea parva carries the blood purified in this portion of the skin back to the sinus venosus, through the vena cutanea magna and ductus Cuvieri.

While emphasizing, in the case of Desmognathus at least, the value of the function of the pharyngo-esophageal apparatus, regulated by breathing movements of nose and throat, I agree with Bethge in the importance of both anterior region of alimentary canal and skin in the respiration of lungless salamanders.

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EXPLANATION OF PLATES.

Abbreviations.

a. car. ext. Arteria carotis externa.
a. car. int. Arteria carotis interna.
a. cut. Arteria cutanea.
a. duod. Arteria duodenalis.
a. epigas. Arteria epigastrica.
a. gas. Arteria gastrica.
a. hep. Arteria hepatica.
a. il. Arteria iliaca.
a. int. com. Arteria intestinalis communis.
a. lien. Arteria lienalis.
a. max. ext. Arteria maxillaris externa.
a. mes. ant. Arteria mesenterica anterioris.
a. oc. Arteria occipitalis.
a. ph. Arteria pharyngea.
a. pul. Arteria pulmonalis.
a. ster. Arteria sternalis.
a. subcl. Arteria subclavia.
a. ver. col. Arteria vertebralis collateralis.
aa. gas. Arteriae gastricae.
aa. gen. Arteriae genitales.
aa. mes. Arteriae mesentericae.
aa. urogen. Arteriae urogenitales.
aa. ver. col. Arteriae vertebrales collaterales.
an. Anus.
ao. Aorta.
b. Place where a capillary branch bends in a plane vertical to the surface and ocular plane.
b. to. pul. Branch of arteria gastrica which anastomoses with arteria pulmonalis.
bl. cor. Blood corpuscle.
blad. Bladder.
cap. Capillary.
cap. sub. cut. Subcutaneous capillary.
cut. Cutis.
cut. bas. Basement layer of cutis.
cutic. Cuticula.
duc. cu. Ductus Cuvieri.
ep. Epidermis.
ept. Epithelium.
ex. op. External opening of slime gland.
gl. Anal gland.
int. Intestine.
kid. Kidney.
liv. Liver.
mid-dor. line. Middorsal line of alimentary canal.
mid-ven. line. Midventral line of alimentary canal.
mus. Muscle.
oes. Esophagus.
ph. Pharynx.
pig. Pigment.
r. abdom. Ramus abdominalis.
rec. Rectum.
sin. ven. Sinus venosus.
sl. gl. Slime gland.
spl. Spleen.
stom. Stomach.
sup. Superficial surface.
tr. ar. Truncus arteriosus.
v. abdom. Vena abdominalis.
v. caud. Vena caudalis.
v. cava post. Vena cava posterioris.
v. cut. mag. Vena cutanea magna.
v. cut. par. Vena cutanea parva.
v. gas. duo. Vena gastrico-duodenalis.
v. haem. Vena haemorrhoidalis.
v. il. Vena iliaca.
v. il. com. Vena iliaca communis.
v. int. Vena intestinalis.
v. jug. ext. Vena jugularis externa.
v. jug. int. Vena jugularis interna.

v. lien. Vena lienalis.
v. lin. Vena lingualis.
v. max. inf. Vena maxillaris inferioris.
v. max. sup. Vena maxillaris superioris.
v. mes. Vena mesenterica.
v. ph. Vena pharyngea.
v. port. hep. Vena porta hepatis.
v. ren. rev. Vena renalis reheventis.
v. subcl. Vena subclavia.
v. ves. Vena vesicularis.
v. gas. Venae gastricae.
vv. mus. Venae musculares.
vv. oes. Venae oesophageae.
vv. ren. adv. Venae renales advehentes.
vert. Vertebra.
I. First arterial arch.
II. Second arterial arch.
IV. Fourth arterial arch.

SEELYE.— Circulatory System of Desmognathus.

PLATE 23.

Fig. 1. Circulatory system of *Desmognathus fusca*. ×5. Ventral view showing the more superficial blood vessels. The ventral body wall is laid back to one side.

Fig. 2. The liver and its blood vessels. Dorsal view.

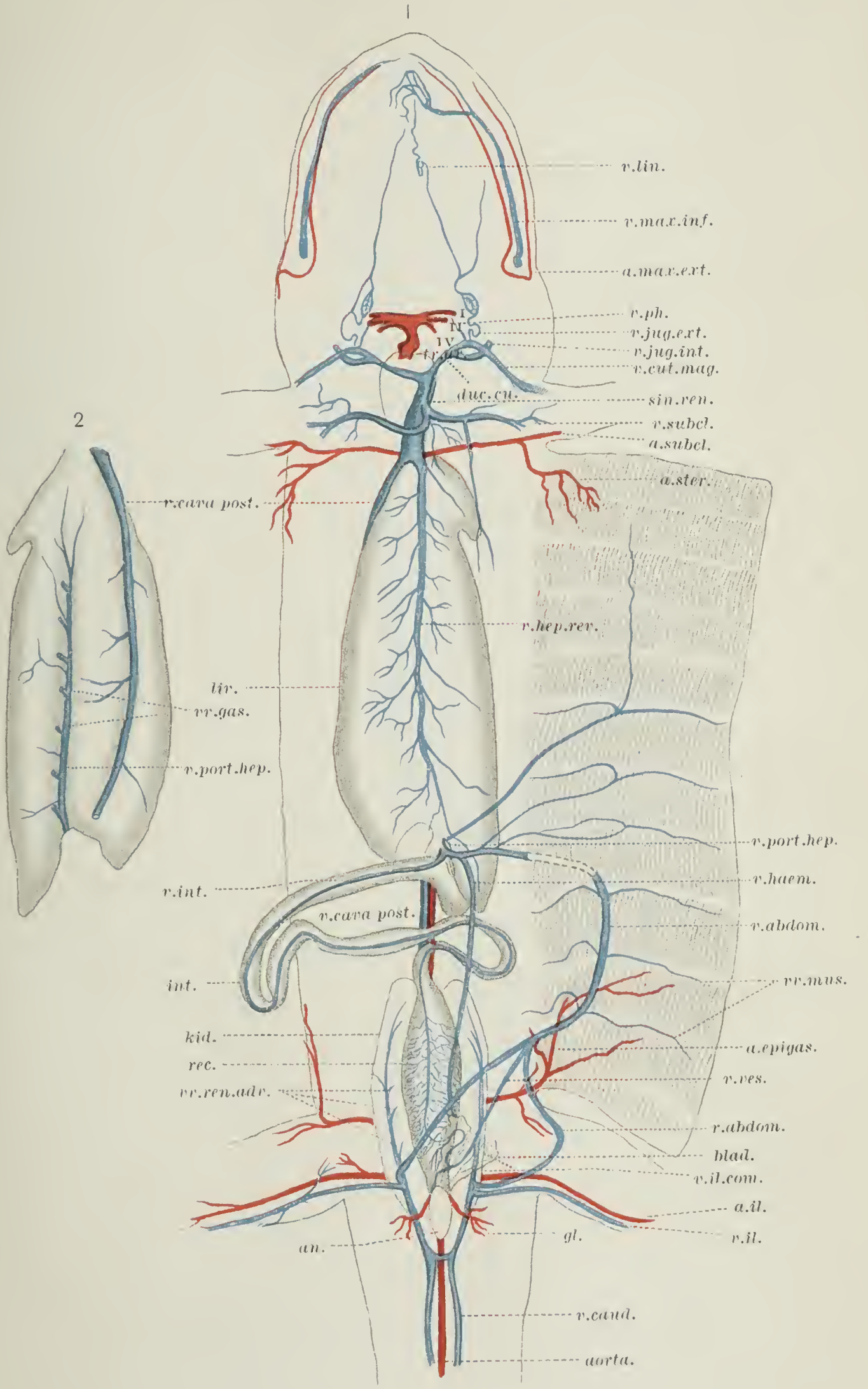

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PLATE 24.

Fig. 3. Circulatory system of *Desmognathus fusca*. ×5. Ventral view showing the deeper blood vessels. The more superficial ventral blood vessels have been removed, and some of the organs displaced.

Fig. 4. Outer surface of esophagus with adjoining parts of pharynx and stomach of *Desmognathus fusca*. The alimentary canal has been opened by a longitudinal incision on the left side, and spread out. The posterior end of this portion of the aorta is slightly displaced to the right. The specimen was injected with a carmine-gelatin mass, and this region cleared with oil of cloves. Drawn with Abbé-Zeiss camera lucida under dissecting lens. ×10, *circa*.

3

4

a.max.ex. sin.
ph.
a.ph.sin.
oes.
aa.gas.
v.gas.
vv.oes.
v.gas.
b.to pul.
ao.
stom.
v.gas.
aa.gas.
mid-dor.line.
mid-ven.line.

I
II
IV
a.car.ext.
a.ph.
a.car.int.
tr.ar.
a.cut.
a.pul.
oes.
a.subcl.
vv.oes.
a.gas.
vv.gas.
ao.
stom.
spl.
v.gas.duo.
liv. lat.
v.port.hep.
a.int.com.
v.lien.
a.hep.
a.lien.
aa.gen.
v.haem.
v.abdom.
v.int.
v.cava post.
a.mesent.
v.mes.
v.ren.rev.
aa.mes.
int.
aa.urogen.
a.epigas.
rec.
v.ren.rev.
a.il.

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PLATE 25.

Fig. 5. Circulatory system of *Desmognathus fusca*. ×5. Ventral view, showing the dorsal blood vessels. The lower jaw, visceral organs, and most of the muscles have been removed.

Fig. 6. Vena cutanea parva and its tributaries, showing the vein turned aside and out from the dorsal side of the head. The small portion of the vena cutanea magna and the point of its connection with vena cutanea parva as in fig. 5.

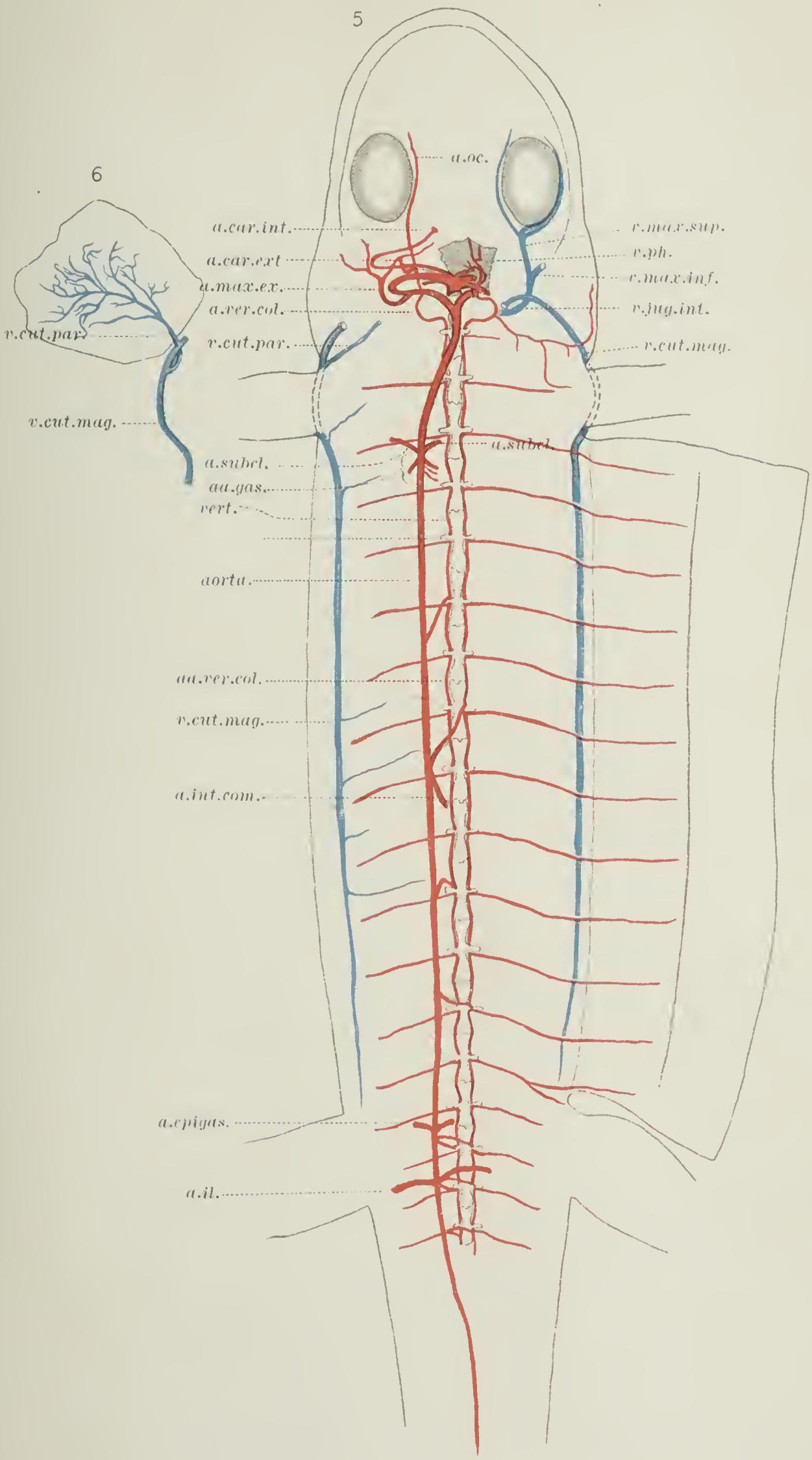

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PLATE 26.

Figs. 7, 8. Cross sections through the integument of *Desmognathus fusca*. Abbé-Zeiss camera lucida, Leitz oc. 1, obj. 6.

Figs. 9, 10. Cross sections through pharyngeal epithelium of *Desmognathus fusca*. Abbé-Zeiss camera lucida, Leitz oc. 1, obj. 6.

Fig. 11. Cross section through esophageal wall of *Desmognathus fusca*. From a specimen injected with a carmine-gelatin mass. Abbé-Zeiss camera lucida, Zeiss oc. 1, obj. DD.

Fig. 12. Surface view of the capillary network in the integument of *Desmognathus fusca*. From a specimen injected with a carmine-gelatin mass. A bit of the integument removed and cleared in oil of cloves. Abbé-Zeiss camera lucida, Zeiss oc. 1, obj. AA.

Fig. 13. Surface view of the capillary network in the pharyngeal epithelium of *Desmognathus fusca*. From a specimen injected with a carmine-gelatin mass. A bit of the epithelium removed and cleared in oil of cloves. Abbé-Zeiss camera lucida, Zeiss oc. 1, obj. DD.

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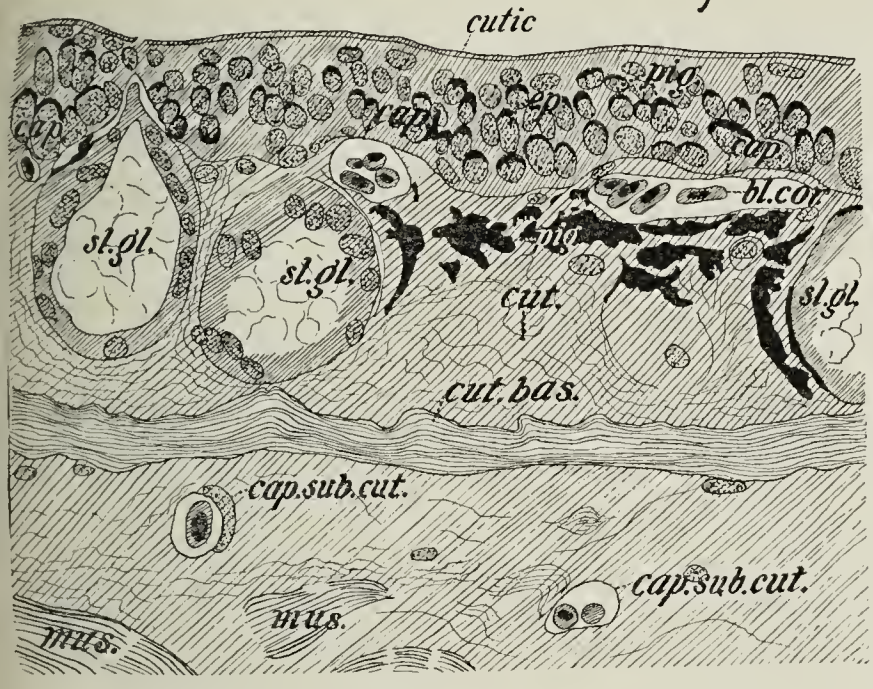

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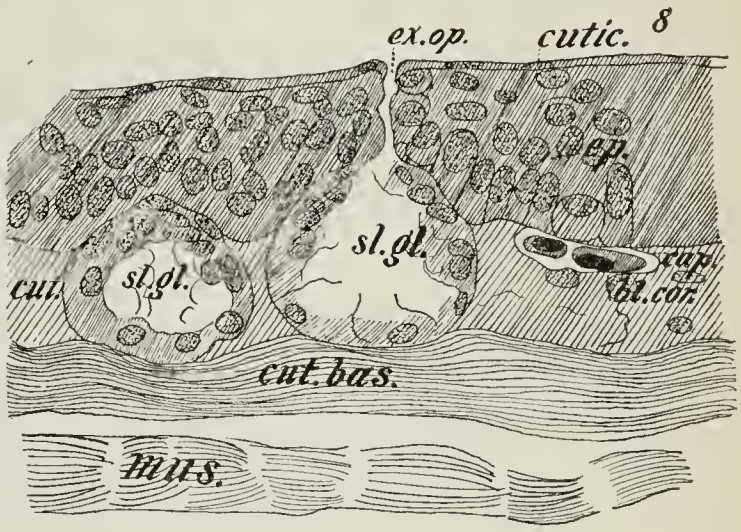

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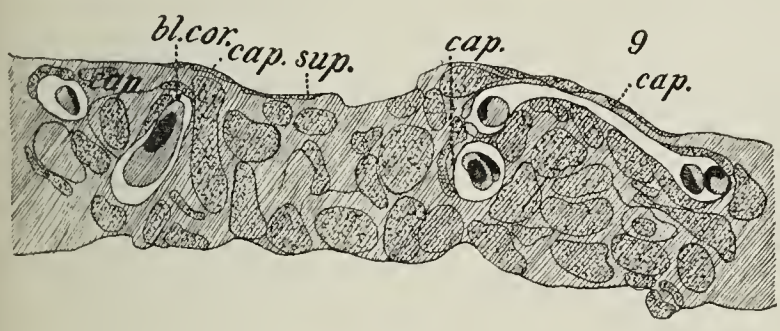

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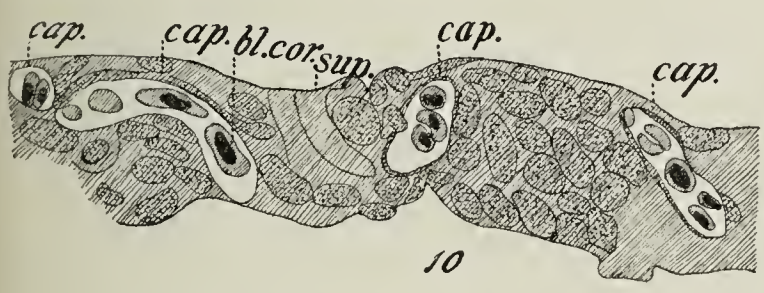

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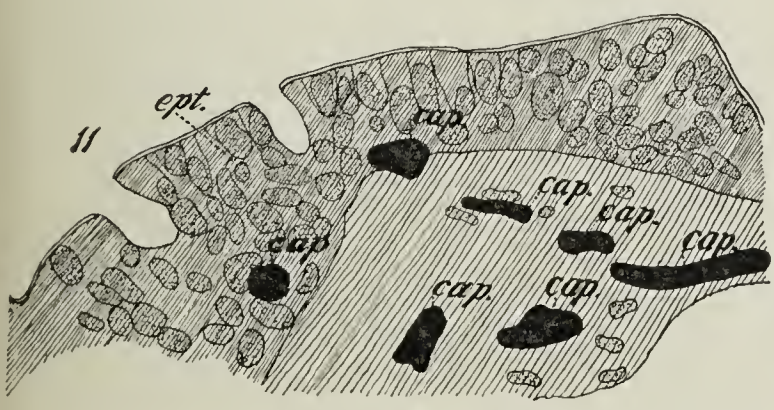

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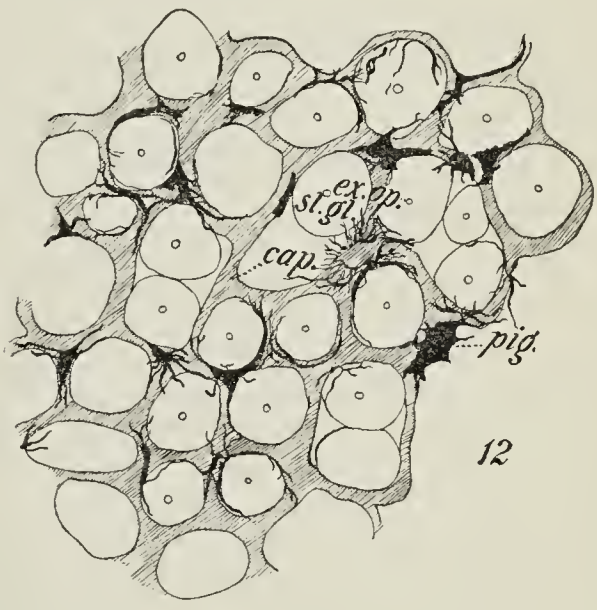

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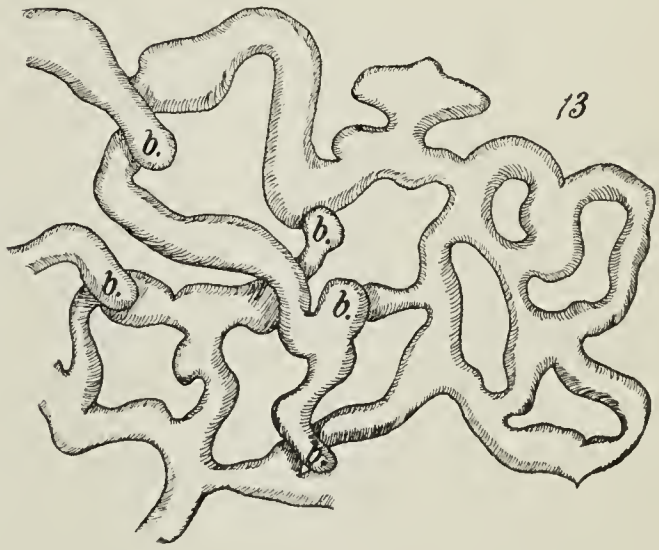

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MARINE OSTRACODA OF VINEYARD SOUND AND ADJACENT WATERS.

By Joseph A. Cushman.

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No. 10.— MARINE OSTRACODA OF VINEYARD SOUND AND ADJACENT WATERS.

BY JOSEPH A. CUSHMAN.

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Introduction.

While both the marine and the fresh-water Ostracoda of European waters have been the subject of extensive monographs for more than half a century, those of the American side of the Atlantic have been little studied. With the exception of a single paper by Brady ('70) on some Ostracoda from the Gulf of St. Lawrence and the description of a single species by Stimpson, there are no papers on our recent species. The reason for the neglect of the marine species is not at all clear for the fresh-water species of the United States have been studied by several workers. Brady and Norman ('89) sum this up as follows: "The Ostracoda of the American side of the Atlantic have not been studied, and our endeavors to procure material from that portion of the area have hitherto failed. A few species from the Gulf of St. Lawrence were described some years ago by Dr. Brady, but nothing whatever is known of the species which inhabit the coasts of the United States." This was written over fifteen years ago but the same condition of things still prevails.

During the summer of 1905, through the kindness of the United States bureau of fisheries I occupied a table at the Wood's Hole station and examined the dredged material. During the two months spent there, twenty-six species were found representing eleven genera. Of these, ten species and one genus are new.

Sources of Material.

The main source of material was the mud and sand in the small scrape dredge of the U. S. S. "Fish Hawk" which worked during the summer in Vineyard Sound. Nearly all of the dredge hauls were in ten fathoms or over and a number of them yielded Ostracoda. The knowledge of the Ostracod fauna would have been far less nearly

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complete had it not been for a single haul, no. 7723. This particular one was very rich in these small Crustacea and hundreds of specimens were picked out from the small amount of the fine sand that was examined. Altogether the material from this one station yielded nineteen of the twenty-six species found and eight of the eleven genera. This one haul gave more species of Ostracods than all the other collecting done during the entire summer. The material from Buzzards Bay was dredged by hand from the Department steamer "Phalarope," mostly in much less than ten fathoms, averaging about four to six fathoms. These hauls were by no means so rich in Ostracoda as those from Vineyard Sound and in the one haul which contained any considerable number of specimens, they were all of one species.

Besides these two sources, material was taken from the Eel Pond at Wood's Hole. This consisted of eel grass, with the mud and other material taken with it in the net. By placing this material in open dishes the Ostracods could easily be picked out with a pipette. Similar procedure was made with good results upon material scraped from the piles of the wharf at the Station and with eel grass and hydroids taken from near the surface in the "Gulf of Canso," across the harbor from the Station. The last locality yielded the only specimens of the Myodocopa seen in the region, with the exception of a single specimen from Vineyard Sound, "Fish Hawk" station 7723.

Periodicity.

While the work done was almost entirely systematic, one thing was incidentally noted which at least suggests an interesting problem. Among the fresh-water Entomostraca certain species have very definite times of appearance and then give way to other species later in the season. That similar conditions may take place among the marine Ostracoda of the region may be suspected from the following casual observations.

On July 15th, material was collected from the Eel Pond, consisting of eel grass, mud, and other accompanying material. From this were obtained many specimens of *Loxoconcha impressa* and a very few of *Cytherois zostericola*. On August 22d from exactly the same part of the Eel Pond, from the same sort of material, and at the same hour of the day even, very many specimens of *Pontocypris edwardsi* were taken and not a single specimen of the two species taken in July.

This would seem to indicate that in this protected, somewhat brackish body of water, there may be a definite succession of species during the season. More detailed observations are necessary, however, to make this more than a suggestion.

Relations of the Fauna.

In the region studied there is apparently a very decided difference in the fauna of the deeper, colder waters of Vineyard Sound and the shallow, warmer portions, such as the harbors, and of the more or less enclosed bodies of water, such as the Eel Pond. The condition of the bottom also seems to have a considerable influence, for certain species are found on sandy bottoms only, others where there is mud only.

Sixteen of the species are identical with those of European waters, including the Mediterranean. Of these all but one, *Cytheridea rubra*, are fairly northern species, most of which extend around the whole northern Atlantic. As far as can be judged, a number of these which occur only in the deeper, colder parts of Vineyard Sound are here near their southern limit. They may be compared with *Cancer borealis*, *Strongylocentrotus dröbachiensis*, and other species which are decidedly northern in all their characters, yet are found in this region in such places. Certain of the species described as new are allied to certain of the European species, as mentioned in connection with the two species of Sarsiella. Others seem to be entirely different and may represent species which are more southern in their range and which are probably confined to this side of the Atlantic.

Many species of Ostracods have been described from shell characters alone and in some of these cases it has been possible to supply figures of the soft parts. In the new species described as many of the parts as possible are figured.

The synonymy is not essentially complete, since only those references are cited which bear on the Atlantic fauna.

TRIBE 1. MYODOCOPA.

The shell is ovate or elongate-ovate, sometimes truncate behind, often produced at the infero-posterior angle; the lower side of the front margin has usually a sinus for the protrusion of the antennae, above which the shell is produced in a more or less rostrate form. The valves are calcareous or thin and submembranaceous with the surface smooth and polished, hispid, or variously sculptured.

The antennulae are not adapted for swimming, but usually bear the sensory appendages. The antenna has a very large basal joint with two branches, one with long plumose setae for swimming, the other rudimentary in the female, but in the male fitted for grasping. The caudal laminae consist of a pair of plates with numerous ungues on the margin, that increase in length toward the end.

This tribe seems to bear a close relation to the Cladocera and especially reminds one of them in the antennal sinus, the caudal laminae, and the method of carrying the ova within the hinder part of the shell.

FAMILY CYPRIDINIDAE.

Shell with a deep incision in front for the protrusion of the antennae (except in the female of Sarsiella). Antennulae stout, 5- to 8-jointed, the fifth joint in the male bearing the large sense organ; antennae with the outer branch usually 9-jointed, inner branch in the male 3-jointed; mandibular foot 5-jointed, terminating in ungues; following limbs maxilliform; caudal laminae oval or subtriangular, with numerous ungues.

Genus SARSIELLA Norman.

Sarsiella Norman, **'68**, p. 293; Sars, **'87**, p. 55; Brady, **'90**, p. 516; G. W. Müller, **'94**, p. 213.
Streptoleberis? Brady, **'90**, p. 515.
Nematohamma Brady and Norman, **'96**, p. 680.

Shell of female without antennal sinus, latero-posterior angle produced; shell of male elongated with antennal sinus and rostral pro-

jection; antennulae 5-jointed, in the male bearing the sense organ at the end of the third joint; sense organ consists of a knob-like thickening at the base bearing many very slender sense hairs; caudal laminae with few (5 to 7) ungues.

Sarsiella americana sp. nov.

Pl. 27, fig. 1–6.

Shell of the female, seen from the side (pl. 27, fig. 1) subovate, nearly circular, the infero-posterior angle produced to form a large, bluntly pointed, conical process; ventral margin broadly rounded; anterior margin slightly sinuous; dorsal margin very irregularly notched and bearing two bluntly pointed spines one of which is bifurcate at the tip. Seen from the front (pl. 27, fig. 2) the shell is broadly truncate at the ventral border and tapers to a blunt point at the dorso-posterior angle; central part of the shell broadest, with a blunt projection at the highest portion.

Surface of the shell with two elevated ridges nearly at right angles to one another, the longest passing from the dorsal margin at the point occupied by the two spinose projections to the middle of the ventral margin. From this ridge a short ridge passes anteriorly to the margin. At the coalescence of these two ridges there is an elevated conical projection forming the highest point of the surface. The whole central part of the shell is raised except at the ventro-posterior angle; the upper surface thus formed, is divided by the raised ridges into three large depressions, of which the anterior ventral is the smallest and the posterior one the largest. The surface has scattered hairs and depressions. Anterior and ventral margins closely set with long, fairly stiff hairs, with a few scattered ones on the dorsal margin. Substance of the shell flexible and submembranaceous; shell when dry shriveling and losing its surface characters.

Height 1.3 mm. Length very slightly greater than the height.

Antennulae (pl. 27, fig. 3) resemble those of *S. capsula* and differ in having three long setae instead of two on the posterior distal angle of the third joint; the last joint with five elongated jointed setae. The natatory branch of the antenna (pl. 27, fig. 4) is like that of the other species of the genus. The mandible (pl. 27, fig. 5) has a single

seta on the posterior side of the first joint. The caudal lamina (pl. 27, fig. 6) has five spines on each plate, that decrease successively in length toward the posterior angle. In this character this species is more like *S. lævis* than like *S. capsula.*

Habitat.— A single female found in the dredgings from "Fish Hawk" station 7723 in the western portion of Vineyard Sound.

In all its characters *S. americana* is more closely allied to the European *S. capsula* than to other described species.

Sarsiella zostericola sp. nov.

Pl. 28, fig. 7–18.

Shell of male (pl. 28, fig. 7) subquadrate, obliquely truncate behind, greatest height somewhat anterior to the middle, equal to seven tenths of the length; ventral margin nearly straight but very slightly sinuous; dorsal margin highly convex centrally; posterior margin widely and obliquely truncate, forming distinct angles at its junction with the adjacent margins. The anterior extremity is bluntly rounded, the lower side rising at an oblique angle from the bottom of the antennal sinus, which is shallow, with the lower edge very gently convex. Surface of the shell at either side raised, the central portion having ridges at either side uniting anteriorly; at the ventral portion is a depressed area bordered by the lateral ridge and a broadly arcuate one situated dorsal to it. The rest of the shell surface is divided into a large anterior and a small posterior area by a ridge extending from the middle of the arcuate one to the dorsal edge of the posterior margin. The three depressed areas are nearly smooth and irregularly punctate. The antennal sinus and the whole ventral border are thickly set with long curved hairs. The anterior end has a few hairs and the posterior margin has a long one at the dorsal angle and one long and two short ones toward the ventral angle.

Seen from above (pl. 28, fig. 8) the greatest width is slightly behind the middle.

Antennulae of the male (pl. 28, fig. 9) have the first joint considerably longer than the second, the former without setae, the latter with one annulated seta toward the distal portion of the front margin. There is an annular depression suggesting another joint at the distal portion of the second; third and fourth joints subequal, the third

with one proximal and one distal annulated seta on the front margin and a pair of short setae on the hind margin, with a third one just above the sensory appendage. This third joint is of the usual type in the male of this genus with its long spreading group of filaments, and from the ventral side at the base, a long annulated seta. Fourth joint with two setae at the frontal distal angle and a longer one from the middle of the distal margin. Fifth joint very short, with five long annulated and sparsely ciliated setae.

Antennae of the male (pl. 28, fig. 10) of the usual type for this genus, the swimming branch with nine setae, two on the last joint; the secondary branch (pl. 28, fig. 11) with two short setae on the upper joint and the next with three stout tooth-like setae between which the end of the terminal claw fits when closed.

The mandibular foot of the male (pl. 28, fig. 12) has a large basal joint; the second and third are subequal, the former with three stout spinose setae on the inner margin and four slender setae, two long and two short, on the outer distal angle; the third joint with a large claw-like seta on the middle of the inner border and three minute spines on the distal anterior angle. Fourth joint short with a long claw-like appendage and with two or three minute spines as in the preceding. Last joint very short, bearing the long terminal claw with a short spine at its base.

The caudal lamina of the male (pl. 28, fig. 13) is five-clawed with the posterior side of each claw heavily spinose, especially near the inner portion; spines in two longitudinal rows.

Copulatory organ of the male (pl. 28, fig. 14) each half ending in a large, blunt chitinous hook with a secondary hook behind it, at either side of which are two sharply pointed spines, and near the upper end two short setae.

Shell of the female (pl. 28, fig. 15) much more rounded than that of the male, the antennal sinus greatly reduced; surface similar to that of the male but less marked.

Antennulae of the female (pl. 28, fig. 16) in general similar to those of the male but without the sensory appendage and the long annulose seta from the same point. The setae above the position of this appendage are in the female long and slender.

The secondary branch of the antenna of the female (pl. 28, fig. 17) is reduced to a single joint having at the tip a stout curved claw and just back from it a small pointed spine.

The mandibular foot of the female (pl. 28, fig. 18) seems to lack the setae of the frontal side of the second joint found in the male but has much more numerous and smaller spines on the posterior side of this joint.

Habitat.— Both males and females of this species were collected by the writer from among eel grass and hydroids (*Pennaria tiarella*), to which they clung. These were from the channel across from Wood's Hole harbor, known locally as the "Gulf of Canso." August 3, 1905.

In the character of the shell surface this in certain points resembles the preceding species, but that species is very much larger, spinose on the border, and different in the minor structural details of the appendages. *S. zostericola* resembles very closely the species described by Brady and Norman as *Nematohamma obliqua* from British waters. It differs from it, however, in the ornamentation of the surface and in the minor structural characters of the appendages.

Genus Cylindroleberis Brady.

Cypridina, of authors.
Asterope Philippi, '**40**, p. 186; Claus, '**76**, p. 94; Sars, '**87**, p. 11; G. W. Müller, '**90**, p. 238; Brady and Norman, '**96**, p. 629.
Cylindroleberis Brady, '**68a**, p. 127; '**68**, p. 464; G. W. Müller, '**94**, p. 216.

Shell oblong or elliptical, polished and smooth; sensory organ of male on antepenultimate joint of antennula, a large stout annulated seta densely clothed with fine hairs; last joint of antennula in male 3-jointed, ending in a recurved claw; mandibular foot with a masticating process at the base.

Cylindroleberis mariae (Baird).

Pl. 29, fig. 19–25.

Cypridina mariae Baird, '**50**, p. 257, pl. 17, fig. 5–7.
Cylindroleberis mariae Brady, '**68**, p. 465, pl. 33, fig. 18–22; pl. 41, fig. 1 a–h.
Asterope mariae Brady and Norman, '**96**, p. 630, pl. 50, fig. 1–6; pl. 51, fig. 11–22; pl. 53, fig. 10–15.
Cypridina oblonga Grübe, '**59**, p. 322, pl. 12.

Asterope oblonga Sars, '87, p. 31, pl. 1, fig. 5–8; pl. 2, fig. 1, 2; pls. 5, 6.
Cylindroleberis oblonga G. W. Müller, '94, p. 219, pl. 4, fig. 14–18, 39, 41, 49–55; pl. 5, fig. 1, 4, 5, 13, 14, 33, 41–44; pl. 8, fig. 4.

Specimens of this species were obtained on August 3, 1905, with *Sarsiella zostericola*. They appear to agree in all respects with European specimens. In certain very minor characters the American specimens differ from the figures of Brady and Norman ('96) but there are certain discrepancies in their figures which may account for these small differences.

No specimens of this species were seen in any of the dredged material, either from Vineyard Sound or from Buzzards Bay during the entire summer. Apparently in this region it lives near the surface as in the locality given.

Length of shell of male 1.8 to 2 mm.

TRIBE 2. PODOCOPA.

Shell never possessing an antennal sinus; antennae simple, apex bearing sharp claws, and used for swimming or walking; maxilla with branchial plate bordered with ciliated setae; heart wanting.

FAMILY CYPRIDAE.

Shell usually without sculpture; antennulae 8-jointed, but by fusion appearing 7- or 6-jointed, usually with long slender setae; antennae 3- to 5-jointed; mandibles strong, apex strongly toothed; two pairs of feet, anterior pair strong, used for locomotion, posterior pair within the shell; caudal rami elongated, with two or three apical claws; copulatory organs symmetrical.

Genus Pontocypris Sars.

Pontocypris Sars, '66, p. 13; Brady, '68, p. 384; '80, p. 35; Brady and Norman, '89, p. 107; G. W. Müller, '94, p. 246.

Shell thin and fragile, higher in front than behind; antennulae 7-jointed, setae longest on last joint, decreasing in length on preceding joints; antennae with four slender claws on the last joint, and

from the apex of the antepenultimate a group of five setae; first pair of feet 5-jointed, claw long; second pair 4-jointed; abdominal rami with two curved claws at the apex besides setae.

Pontocypris edwardsi sp. nov.

Pl. 30, fig. 26–34.

Shell, seen from the side, subtriangular, highest in the middle, height equal to more than half the length; dorsal margin strongly arched, highest in the middle; seen from below, the outline is elliptical, widest in the middle; valves smooth, thickly clothed with fine hairs.

Antennulae with four setae from the basal joint; antennae of the usual type for the genus; terminal claw of the maxillary foot long and slender, at least equalling in length the preceding three joints; terminal claw of the first pair of feet very long and slender, somewhat less than the total length of the preceding four joints, pectinated toward the outer end; pectinated seta of the second foot of medium length with at least twelve secondary processes; abdominal ramus with the outer of the two terminal claws only about one half the length of the inner one.

Length 0.85 mm.; height 0.47 mm.

Habitat.— Collected in considerable numbers in the Eel Pond, Wood's Hole, August 22, 1905, from material seined by Mr. Vinal N. Edwards and the writer. All the specimens dissected were females. This was the only species present at this date, although a few weeks previously, in exactly the same part of the pond and at the same time of day, two other species were taken while the one here described was not seen at all. The European species of this genus seem to prefer muddy bottoms of protected or even brackish bodies of water. Our species is therefore very similar in its habits, for it was found nowhere in the region during the summer's collecting except in this one locality, the Eel Pond, where such conditions prevail.

FAMILY CYTHERIDAE.

Shell usually hard and calcareous, surface typically rough or sculptured; antennulae and antennae not fitted for swimming, the latter lacking the long brush of setae present in the foregoing family; three

pairs of feet directed forwards, usually very similar, increasing in length to the posterior ones, ends fitted with stout claws for crawling; postabdomen rudimentary; copulatory organs of male large and complicated.

Genus Cytherois W. Müller.

Paradoxostoma Sars, '66, p. 91; Dahl, '88, p. 629. In part.
Cytherois W. Müller, '84, p. 15; G. W. Müller, '94, p. 309; Brady and Norman, '89, p. 227.

Shell thin, elongated, without sculpture; antennulae long and slender, second joint longer than any of the others; antennae 5-jointed, the last joint with a strong claw, flagellum 3-jointed; feet small and slender, joints 2 to 4 of third feet hairy on the anterior border.

Cytherois zostericola sp. nov.

Pl. 31, fig. 35–41.

Shell, seen from the side, elongated, oval, width nearly equal to half the length; surface smooth, shell yellowish white.

Antennulae with three short setae from the middle of the second joint; at the end of the penultimate joint a group of three setae on one side with a single seta on the other; last joint with four slender setae. Jaw of mandible with one large tooth and indications of three smaller ones.

Length 0.5 mm.

Habitat.— Collected in the Eel Pond, Wood's Hole, July 15, 1905, in exactly the same place that *Pontocypris edwardsi* was taken later in the summer. The species was not met with at any other locality nor in any of the dredgings.

Genus Xestoleberis Sars.

Xestoleberis Sars, '66, p. 66; Brady, '68, p. 437; '80, p. 124; G. W. Müller, '94, p. 332.

Shell smooth and polished, ornamentation consisting of scattered

raised papillae, shell lower anteriorly than posteriorly, ventral border with a distinct re-entrant, widest posteriorly; antennulae 6-jointed, joints decreasing in size and length toward the outer end, setae all simple; antennae 4-jointed; feet short; animal viviparous.

Xestoleberis depressa Sars.

Xestoleberis depressa Sars, '**66**, p. 68; Brady, '**68**, p. 438, pl. 27, fig. 27–33; '**70**, pp. 450, 453; Brady and Crosskey, '**71**, pp. 61, 63; Brady, Crosskey, and Robertson, '**74**, p. 190, pl. 7, fig. 13–19; Brady, '**80**, p. 124, pl. 31, fig. 1 a–g; Brady and Norman, '**89**, p. 188.

Of this species but a few specimens were found and these were dead shells, Vineyard Sound, "Fish Hawk" station 7723. This species appears to be a northern one and the few specimens found here may be well toward its southern limit as in the case of *Cancer borealis*, *Strongylocentrotus dröbachiensis*, and other strictly northern species found in the deeper, colder waters of the Sound. It is reported by Brady ('**70**) from the Gulf of St. Lawrence but the record was somewhat in doubt according to that author. Brady and Crosskey ('**71**) record the species from the post-Tertiary clays of Portland, Maine. In the north it is found in Davis Strait, Greenland, and Spitzbergen and follows down the coast of western Europe into the Mediterranean.

Genus Loxoconcha Sars.

Loxoconcha Sars, '**66**, p. 61; Brady, '**68**, p. 432; '**80**, p. 116; G. W. Müller, '**94**, p. 342.

Shell usually with a decided projection on the dorso-posterior angle with a corresponding re-entrant behind it; ends and ventral margin extended into a flattened rim; antennulae 6-jointed, slender, last joint with a group of long slender setae; antennae 4-jointed, third joint much the longest; feet long and slender, alike in both sexes.

Loxoconcha guttata (Norman).

Pl. 31, fig. 42–48; pl. 32, fig. 56.

Cythere guttata Norman, '**65**, p. 19, pl. 6, fig. 9–12.
Loxoconcha guttata Brady, '**68**, p. 436, pl. 27, fig. 40–44; Brady, Crosskey,

and Robertson, '74, p. 186, pl. 8, fig. 5–7; Brady, '80, p. 120, pl. 29, fig. 1 a–f; Brady and Norman, '89, p. 184.

Loxoconcha granulata Sars, '66, p. 64; Brady, '68, p. 434, pl. 25, figs. 51, 52; Brady and Crosskey, '71, pp. 61, 63.

Living specimens of this species were dredged in Vineyard Sound, "Fish Hawk" station 7723, and in Buzzards Bay, "Phalarope" station 82.

All the specimens seen were of the type called by Sars *L. granulata* which Brady and Norman consider as the younger stage of *L. guttata* (Norman). The animal of the *guttata* type of shell needs to be fully studied to make certain that the two are really the same species. A fairly complete series of figures of the appendages is here given, including that of the copulatory organ of the male.

This species does not seem to extend so far north as does the preceding, being found from Norway through the Mediterranean. Brady and Crosskey ('71) record it from the post-Tertiary clays of Portland, Maine.

Loxoconcha impressa (Baird).

Pl. 32, fig. 49–55.

Cythere impressa Baird, '50, p. 173, pl. 21, fig. 9.

Loxoconcha impressa Brady, '68, p. 433, pl. 25, fig. 35–40; pl. 40, fig. 4; Brady and Crosskey, '71, p. 61–63; Brady, Crosskey, and Robertson, '74, p. 185, pl. 8, fig. 1–4; Brady and Norman, '89, p. 183, pl. 23, fig. 7.

Loxoconcha rhomboidea Sars, '66, p. 62 (*non C. rhomboidea* Fischer); Dahl, '88, p. 621, pl. 18, fig. 72–89.

Cythere viridis Lilljeborg, '53, p. 168.

Cythere carinata Brady, '65, p. 190.

This species seems to be very common in the region, especially in comparatively shallow water, where it appears to live up among the eel grass and hydroids rather than on the bottom. It was taken in the Eel Pond, Wood's Hole, on July 15, 1905, in numbers, from hydroids and other material scraped from the piles of the wharf of the United States fish commission station, and in great numbers among eel grass and hydroids near the surface from the "Gulf of Canso," August 3, 1905. It was also found living in material dredged in Vineyard Sound, "Fish Hawk" stations 7716, 7723. In these deeper places it was rarely met with and then only as occasional specimens.

The species is found in Europe from Norway and Finmark southward into the Mediterranean. This is the first record for the western Atlantic coast.

Genus Cythere O. F. Müller.

This genus has been divided by later writers according to morphological characters but as the soft parts were not present in the following species it is thought best to leave the species under the original genus until the soft parts are known.

Cythere dawsoni Brady.

Pl. 35, fig. 84–85.

Cythere dawsoni Brady, '**70**, p. 453, pl. 19, fig. 8–10; Brady and Crosskey, '**71**, p. 64, pl. 2, fig. 5–7; Brady and Norman, '**89**, p. 166, pl. 15, fig. 14–15.

Several shells were found which seem to belong to this species although the original figures are incomplete in details. The shells were found in the deeper part of Vineyard Sound, "Fish Hawk" station 7723. The species is probably a northern one on our coast, and was described originally by Brady from the Gulf of St. Lawrence and found fossil by Brady and Crosskey at Portland, Maine, and at Montreal.

Genus Cytheridea Bosquet.

Cytheridea Bosquet, '**52**, p. 37; Sars, '**66**, p. 55; Brady, '**68**, p. 421; '**80**, p. 111; G. W. Müller, '**94**, p. 359.

Shell smooth, sometimes slightly ornamented with raised papillae or impressed punctae, left valve usually the larger; antennulae 5-jointed, bearing short strong spines, end joint bearing but three setae; antennae 4-jointed, flagellum shorter in the female than in the male; mandibular palp 4-jointed, the next to the last joint at about the middle suddenly broadening on the dorsal border; from the outer angle thus formed springs a group of setae; branchial plate of maxilla without aberrant rays; in the male the first and second right and left feet differ, the second right foot being rudimentary, without a terminal claw.

Cytheridea rubra G. W. Müller.

Pl. 33, fig. 57–61; pl. 34, fig. 78.

Cytheridea rubra G. W. Müller, '**94**, p. 360, pl. 30, fig. 24–27, 29, 30, 34–39, 46, 48.

The American specimens seem to be like the Mediterranean ones in all respects, both in the characters of the shell and those of the appendages. According to Müller it does not seem to be a very common species in the Mediterranean, for he found it but once, then in ten fathoms.

Shells of this species were found in Buzzards Bay, "Phalarope" station 102, and it was found living in Vineyard Sound, "Fish Hawk" stations 7685, 7686, 7723, 7725.

This species, being found in the Mediterranean and not noted from the rest of Europe, may be a more southern type. It seems to be fairly well distributed in the Wood's Hole region.

Cytheridea papillosa Bosquet.

Pl. 33, fig. 65–66.

Cytheridea papillosa Bosquet, '**52**, p. 42, pl. 2, fig. 5 a–d; Brady, '**68**, p. 423, pl. 28, fig. 1–6; pl. 40, fig. 1; '**70**, p. 450; Brady and Crosskey, '**71**, pp. 61, 62, 63; Brady, Crosskey, and Robertson, '**74**, p. 176, pl. 6, fig. 12–15; Brady and Norman, '**89**, p. 173.
Cythere debilis Norman, '**65**, p. 15, pl. 5, fig. 5–8.
Cyprideis bairdii Sars, '**66**, p. 52.

This species was met with but once and then the empty shell only was found. This one locality, "Fish Hawk" station 7723, was in the deeper part of Vineyard Sound as might have been expected for this is a decidedly northern species whose range extends northward in Davis Strait to lat. 69° 31′ N., Baffin's Bay, Iceland, and Spitzbergen. It is common on the northern coasts of the British Isles but not on the southern coasts, that being apparently nearly the southern limit. It has been recorded from the Gulf of St. Lawrence by Brady ('**70**) and from the post-Tertiary clays of Portland and Saco, Maine, and from Montreal by Brady and Crosskey ('**71**).

Cytheridea punctillata Brady.

Cytheridea punctillata Brady, **'65**, p. 189, pl. 9, fig. 9–11; **'68**, p. 424, pl. 26, fig. 35–38; **'70**, p. 450; Brady and Crosskey, **'71**, pp. 62, 63; Brady Crosskey, and Robertson, **'74**, p. 177, pl. 6, fig. 1–11; Brady and Norman, **'89**, p. 173.
Cyprideis (*?*) *pulchra* Brady, **'66**, p. 368, pl. 58, fig. 3 a–c.
Cyprideis proxima Sars, **'66**, p. 54.

Shells of this species were found with *C. papillosa* at "Fish Hawk" station 7723. In Europe this species has a somewhat more southern range than the preceding being recorded from the Mediterranean. Brady (**'70**) records this species from the Gulf of St. Lawrence and Brady and Crosskey (**'71**) record it from the post-Tertiary of Montreal.

Cytheridea seminuda sp. nov.

Pl. 33, fig. 62–64; pl. 34, fig. 76–77.

Shell, seen from the side, elongate, highest toward the posterior end, height somewhat less than half the length, dorsal margin very gently curved, sloping somewhat abruptly at either end; seen from above, elongate, ovate, widest posteriorly, subacute in front, broadly rounded behind. Surface of dorsal half smooth with numerous small rounded papillae, ventral half sculptured, with indented polygonal areas obscurely linear in their arrangement, especially toward the ventral border. Lucid spots six in number, four grouped, the other two in front, the dorsal one much the larger of the two.

Antenna of the male with a peculiar comb-like claw on the end of the penultimate joint; second pair of feet differing much on the two sides in the male, right foot 3-jointed, the last two joints slender and rudimentary, without a terminal claw and without the setae at the end of the second joint.

Length of the shell 1.2 mm.

Habitat.— Found in the deeper parts of Vineyard Sound, "Fish Hawk" stations 7723, 7725.

The peculiar pectinated claw of the antenna of the male, and the two different sorts of ornamentation of the shell will at once distinguish the species.

Cytheridea americana sp. nov.

Pl. 33, fig. 67; pl. 34, fig. 68–75.

Shell, seen from the side, elongate, highest in front of the middle, height less than half the length; dorsal margin gently arched in the middle, sloping very abruptly at the posterior end to form a dorso-posterior angle; anterior end more evenly rounded; both ends of the shell extended at the ventral portion; seen from above, elongate-ovate, widest in the middle, both ends somewhat truncately rounded; surface of the shell punctate, with large, irregularly scattered impressed areas with one or more masses of pigment in each, these areas most abundant anteriorly; besides these the anterior half has about nine large lucid spaces.

Antennulae with three groups of hairs on the second joint; antennae of the usual type, but without the short setae in the middle of the outer border of the third joint; claw of the mandible with the outer tooth much longer than the others, otherwise much like that of *C. rubra*; feet slender with the second joint of the left foot in all three pairs with hairs on the outer border, posterior seta of first joint of first foot large and club-shaped; copulatory organ of the male with a very large, oval, basal mass, outer portion somewhat sharply acuminate.

Length of the shell 1 mm.

Habitat.— Dredged alive from the deeper part of Vineyard Sound, "Fish Hawk" station 7723.

The surface characters of this species, with its fine punctae, coarser, impressed, pigmented areas, and the larger lucid areas will serve to distinguish it.

Genus Cythereis Sars.

Cythere, in part, of authors.
Cythereis Sars, **'66**, p. 35; G. W. Müller, **'94**, p. 364.

Shell strongly calcareous, usually richly sculptured; antennulae usually 6-, rarely 5-jointed; antennae 4-jointed, flagellum short in the female; mandibular palp 4-jointed; first pair of feet differing on the two sides of the body in the male.

Cythereis emarginata Sars.

Pl. 35, fig. 79–82.

Cythereis emarginata Sars, '**66**, p. 38; Dahl, '**88**, p. 609, pl. 16, fig. 13–26, 30.
Cythere emarginata Brady, '**68**, p. 475; '**70**, p. 450; Brady and Crosskey, '**71**, pp. 61, 62; Brady, Crosskey, and Robertson, '**74**, p. 166, pl. 5, fig. 1–6; Brady and Norman, '**89**, p. 163, pl. 16, fig. 1–2.

Specimens of this species were dredged alive from Buzzards Bay, "Phalarope" station 87, and from Vineyard Sound, "Fish Hawk" stations 7710, 7723, 7727, 7729. Specimens showed very considerable differences in the depth of the sculpturing of the shell surface but in the abundance of the material the extremes were well bridged over. The figure represents nearly the extreme of the deeply impressed sculpturing.

C. emarginata is a northern species, having been obtained within the Arctic circle. It is recorded by Brady ('**70**) from the Gulf of St. Lawrence, and by Brady and Crosskey ('**71**) from the post-Tertiary of Portland, Lewiston, and Saco, Maine.

Cythereis tuberculata Sars.

Pl. 36, fig. 108–109.

Cythereis tuberculata Sars, '**66**, p. 37.
Cythere tuberculata Brady, '**68**, p. 406, pl. 30, fig. 25–41; '**70**, p. 450; Brady, Crosskey, and Robertson, '**74**, p. 164, pl. 5, fig. 7–12; Brady and Norman, '**89**, p. 161.
Cythere mutabilis Brady, '**66**, p. 377, pl. 59, fig. 12–14.

The shells of this species were obtained for the most part in the deeper and colder parts of Vineyard Sound, "Fish Hawk" stations 7686, 7723. At the former station a single living individual was taken.

The animal of this species has not been sufficiently studied and for this reason figures of the antennulae, antenna, and second leg are here given.

This is a widely distributed species ranging from lat. 78° N. to the Mediterranean on the other side of the Atlantic. Brady ('**70**) records the species from the Gulf of St. Lawrence. Very probably this is

near its southern limit in Vineyard Sound as are many other of the Crustacea.

Cythereis canadensis (Brady).

Cythere canadensis Brady, '**70**, p. 452, pl. 19, fig. 4–6; Brady and Norman, '**89**, p. 166, pl. 15, fig. 14–15.

Shells of this species were dredged from "Fish Hawk" station 7723. No living specimens were found. From the known range of this species it is in all probability a northern one, being described by Brady ('**70**) from the Gulf of St. Lawrence and later found in Davis Strait, lat. 66° 55′ N., long. 55° 30′ W., 57 fathoms.

Cythereis dunelmensis Norman.

Cythereis dunelmensis Norman, '**65**, p. 22, pl. 7, fig. 1–4.
Cythere dunelmensis Brady, '**68**, p. 416, pl. 30, fig. 1–12; '**70**, p. 450; Brady and Crosskey, '**71**, pp. 61, 63; Brady, Crosskey, and Robertson, '**74**, p. 168, pl. 5, fig. 13–20; pl. 11, fig. 36–37; Brady and Norman, '**89**, p. 168.
Cythereis horrida Sars, '**66**, p. 45.

Shells referred to this species were obtained in the deeper parts of Vineyard Sound, "Fish Hawk" stations 7725, 7727.

This again is a northern species, and is found in British waters and as far north as Spitzbergen, Iceland, and Baffin's Bay. Brady and Crosskey ('**71**) record this species from the post-Tertiary clays of Saco and Portland, Maine.

Cythereis concinna (Jones).

Cythere concinna Jones, '**56**, p. 29, pl. 4, fig. 7 a–f; Brady, '**68**, p. 408, pl. 26, fig. 28–33; pl. 38, fig. 7; '**70**, p. 450; Brady and Crosskey, '**71**, pp. 61, 62; Brady, Crosskey, and Robertson, '**74**, p. 160, pl. 4, fig. 1–20; Brady and Norman, '**89**, p. 162.
Cythereis clavata Sars, '**66**, p. 39.

A single shell apparently belonging to this species was dredged in Vineyard Sound, "Fish Hawk" station 7723. Like the preceding species it is a northern one. Brady ('**70**) records it from the Gulf of

St. Lawrence and Brady and Crosskey ('71) record it from the post-Tertiary of Portland, Maine.

Cythereis albomaculata (Baird).

Pl. 35, fig. 83.

Cythere albomaculata Baird, '50, p. 169, pl. 20, fig. 7; Brady, '68, p. 402, pl. 28, fig. 33–39; pl. 39, fig. 3 a–k; Brady, Crosskey, and Robertson, '74, p. 149, pl. 9, fig. 1–4; Brady and Norman, '89, p. 138.
Cythere alba Baird, '50, p. 170, pl. 20, fig. 6.

Living specimens of this species were obtained but once, and then from hydroids and other material scraped from the piles of the wharf of the United States fish commission station at Wood's Hole. In contrast to the preceding species it is more southern, and occurs almost entirely in the littoral and laminarian zones and in tidal rivers. As these portions of the area were not fully investigated it may be found to be common in the region. There were certain discrepancies between the specimens and the published figures of the animal parts and more material may show it to be an entirely distinct species.

Cythereis villosa Sars.

Cythereis villosa Sars, '66, p. 42.
Cythere villosa Brady, '68, p. 411, pl. 29, fig. 29–32; '70, p. 450; Brady, Crosskey, and Robertson, '74, p. 157, pl. 3, fig. 7–13; Brady and Norman, '89, p. 146.

The shells of this species are fairly common in the deeper parts of Vineyard Sound, and were especially noted at "Fish Hawk" stations 7723 and 7727. It is a northern species on the European coast and is recorded by Brady ('70) from the Gulf of St. Lawrence. It also occurs in the post-Tertiary of Canada.

Cythereis phalaropi sp. nov.

Pl. 35, fig. 86–94; pl. 36, fig. 95–96.

Shell, seen from the side, ovate, greatest height in front, equal to

half the length, anterior extremity broad, well rounded, posterior much narrower, produced most above, dorsal margin nearly straight, ventral margin arcuate in front, slightly sinuate at about the middle, posteriorly rapidly rising to about three fourths the entire height of the shell; borders of the shell smooth, without teeth. Seen from below the outline is ovate, twice as long as broad, greatest width in front of the middle. Surface of the valves for the most part smooth, posterior border produced slightly to form a narrow flattened rim; ends with scattered hairs and the whole surface sparsely set with short hairs. Color pattern peculiar, consisting of a light band at either end and a large light area occupying the lower middle portion of the shell, this latter broken by bands of darker color which make up the rest of the shell. Below is a club-shaped area of very dark color, and the main part of the shell is made up of this darker color.

Antennulae with two groups of long hairs on both the first and the second joints; mandibular palp of the type given by Müller for this genus; maxilla with a ciliated seta from the outer limb besides the usual setae. The lower border of the first joint of the first and second pairs of feet thickly set with long hairs, especially long and dense in the first pair. Feet similar on the two sides except that in the first two pairs the last three joints of the left feet are much stouter than those of the right feet. Terminal claws of all the feet with a swollen base and a very slender outer portion.

Habitat.— Found but once, then living, in Buzzards Bay, "Phalarope" station 129; apparently not common.

Cythereis arenicola sp. nov.

Pl. 36, fig. 97–107.

Shell, seen from the side, quadrangular, of almost equal height throughout, slightly higher anteriorly, height one half the length, ends broadly rounded, anterior end produced slightly below; viewed from below, elongate-ovate, widest in front of the middle, width slightly less than half the length; from the inside the borders of the shell are seen to be thickened and the pore canals extend in through this border; there are also local thickenings in the upper portion of the shell below the hinge. Surface of the shell with scattered, irregularly shaped areas, usually each with a single hair. Figure 100

(pl. 36) shows the condition of these areas which have three or four rows of minute papillae from one of which springs the fine hair. These areas are more transparent than the rest of the shell. Besides these areas there are scattered papillae which are pigmented, most frequent near the ends and the dorsal border. They have a slightly swollen upper end when seen in side view. The ends of the shell have both a series of longer hairs at the border.

The antennulae have two groups of hairs on the first and three on the second joint, the latter also has a short seta near the upper end of the outer margin besides the larger annulated seta at the lower end of the inner margin; the rays of the branchial plate of the maxilla are somewhat irregularly placed on the anterior border; the third foot has the terminal claw at least as long as the sum of the preceding two joints; basal joint of the first foot only with hairs; copulatory organ of the male with the basal portion divided into two parts, the upper of the two irregularly triangular, the lower portion broadened laterally; outer portion of the organ elongated, complex.

Length of shell 1 mm.

Habitat.— Found to be fairly common on sandy bottoms in Vineyard Sound, "Fish Hawk" stations 7710, 7723.

Cythereis vineyardensis sp. nov.

Pl. 37, fig. 110–114.

Shell, seen from the side, quadrangular, highest in front, greatest height about half the length; dorsal border nearly straight, with small irregularities, ventral border also nearly straight, somewhat sinuous, posterior evenly but slightly arched, anterior border rounded, produced slightly below the middle. Seen from above the shell is irregularly elongate, ovate, widest just behind the middle, width about two fifths of the length. Surface of the shell sculptured, ends with a series of bordering teeth and scattered hairs, whole surface of the shell except the borders raised, antero-ventral and dorsal borders of this raised portion with rounded projections; raised area obliquely truncated posteriorly; median line of the shell with a raised ridge on which are numerous projections, most numerous anteriorly.

The last joint of the antennula with three long slender setae; first foot 2-jointed, outer joint very long, swollen in the middle, with a

short stout strongly curved claw; third foot with the second and third joints fringed at the ends with short, closely set hairs.

Length of the shell 0.9 mm.

Habitat.— Found in Vineyard Sound, "Fish Hawk" station 7723. The soft parts were not well preserved; only those figured were in condition for study. The structure of the first foot seems very much like that of Krithe but the other portions of the animal are much more like Cythereis.

Genus Cytherideis Jones.

Cytherideis Jones, **'56**; Brady, **'68**, p. 454; **'80**, p. 146; Brady and Norman, **'89**, p. 226; G. W. Müller, **'94**, p. 380.

Shell elongated, subovate, tapering and depressed anteriorly, antennulae slender, with few setae, last joint with six short terminal setae, penultimate and antepenultimate joints each bearing a single apical seta; mandible slender and curved; maxilla with the first segment much stouter and of greater size than the three others.

Cytherideis fasciata (Brady and Robertson).

Pl. 37, fig. 114a–118.

Cytherideis subulata var. *fasciata* Brady and Robertson, **'74**, p. 55, pl. 1, fig. 12–13.

This seems to be a valid species rather than a form of *C. subulata* as originally described. In Vineyard Sound no specimens of typical *C. subulata* were found, while living examples were dredged which exactly correspond to those described as var. *fasciata*. The dark bands are of the same size and shape and the epidermis is reticulated; the areas thus cut off are minutely punctate. The specimens, too, are larger than *C. subulata*.

Antennulae with groups of hairs on each side of the elongated second joint; antennae with the second joint set with a number of long slender scattered setae on the outer border, third joint very much elongated; first foot with very stout first joint, the main seta of the upper border being very long and stout, seta of the ventral side also stout, last three

joints slender; maxilla with the outer joint stout, bearing three short, stout spines on its inner margin.

Habitat.— Specimens from Vineyard Sound, "Fish Hawk" station 7723. Original specimens described from the Scilly Islands.

Pseudocytheretta gen. nov.

The essential characters of Pseudocytheretta are as follows: inner border of shell irregular with an S-shaped line as in Cytheretta but less prominent; a similar angle below the adductor muscle insertion, and likewise with the flat arch of Cytheretta; flagellum of the antenna 3-jointed; first foot of the male with a seta on the hinder border, left and right first feet of male greatly different, the last joint of the first foot of the right side being elongated and greatly broadened on the inner border, the extension thus formed equalling in length the sum of the two joints preceding. Type of genus, *Pseudocytheretta edwardsi* sp. nov.

Müller's description of the genus Cytheretta is here given in free translation: "Genus near Cythereis, but differs from it in the following points. The inner border has a very irregular course, building on the anterior border a strong S-shaped line, on the ventral border below the adductor muscle insertion an angle reaching far downward, behind it an irregular, flat arch opening downward. It fails of entirely reaching the line of joining. Flagellum of the antenna in both sexes 3-jointed. First foot of the male on the hinder border without a seta, second foot of the male and female on the outer border with but one seta (besides the seta at the 'knee'). Penis with long, free, copulatory tube."

Pseudocytheretta edwardsi sp. nov.

Pl. 38, fig. 119–132.

Shell with dorsal and ventral margins nearly parallel, anterior end produced somewhat below, posterior end more produced above giving an oblique appearance to the whole shell; both ends broadly rounded. Surface smooth with scattered hairs, ends slightly hairy. In a fresh condition the middle portion toward the sides and below is a clear chestnut brown with the rest of the shell a delicate pink. In old shells this color is lost by thickening of the shell substance.

Antennulae with a long first joint, bearing a double cluster of hairs near the upper posterior margin and a smaller one on the outer end of the anterior margin, second joint large, swollen in the middle posteriorly; on this broadest part a cluster of hairs, another cluster on the proximal end of the opposite margin. Flagellum of the second antenna 3-jointed, the last joint the longest; first joint broadest at its outer end; third joint long; from the end of the second joint are two setae, one long, the other short. Mandible and maxilla as in Cytheretta. First joint of first feet broad, densely haired on the hinder border and with a large ciliated seta, densely haired; anterior border with four setae as in Cythereis. Left foot with the outer three joints and claw as in Cytheretta, right foot with the second joint shorter and broader than the left, third joint shorter and more than twice as broad as in the left, with two groups of bristles on the lower border of either side. Fourth joint very broad, front margin somewhat extended laterally, hinder portion extended distally to nearly four times the length of the rest of the joint and greatly broadened out, joint above the claw fringed with long hairs. Claw much shorter and very much broader than in the left and sharply acuminate. Second foot with a group of hairs near the seta of the hinder margin of the first joint and a seta near the middle of the side. Third foot also with a group of hairs near the seta of the hinder margin in the first joint; second joint with a group of very long hairs on the frontal margin and a group of shorter ones on the hinder margin. All the feet have a short spine at the end of the third joint. Copulatory organ of the male in the figure somewhat flattened, in its essentials similar to that of Cytheretta.

Habitat.— This species was first found in a dredge haul made by Mr. Vinal N. Edwards and the writer in 17 fathoms, sandy bottom, in Vineyard Sound, off Menimsha Bight, on July 13, 1905. Later it was found to be the most common Ostracod in the region; specimens were obtained in Buzzards Bay, "Phalarope" station 102, and in Vineyard Sound, "Fish Hawk" stations 7686, 7710, 7724, 7727, 7729. It seems to be confined to fairly deep water and as a rule to sandy bottoms.

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EXPLANATION OF PLATES.

PLATE 27.

Sarsiella americana sp. nov.

Fig. 1. Shell of female seen from the side. × 45.
Fig. 2. Shell of female seen from the front. × 45.
Fig. 3. Antennula of female. × 125.
Fig. 4. Natatory branch of antenna of female. × 125.
Fig. 5. Mandibular foot of female. × 125.
Fig. 6. Abdominal lamina of female. × 125.

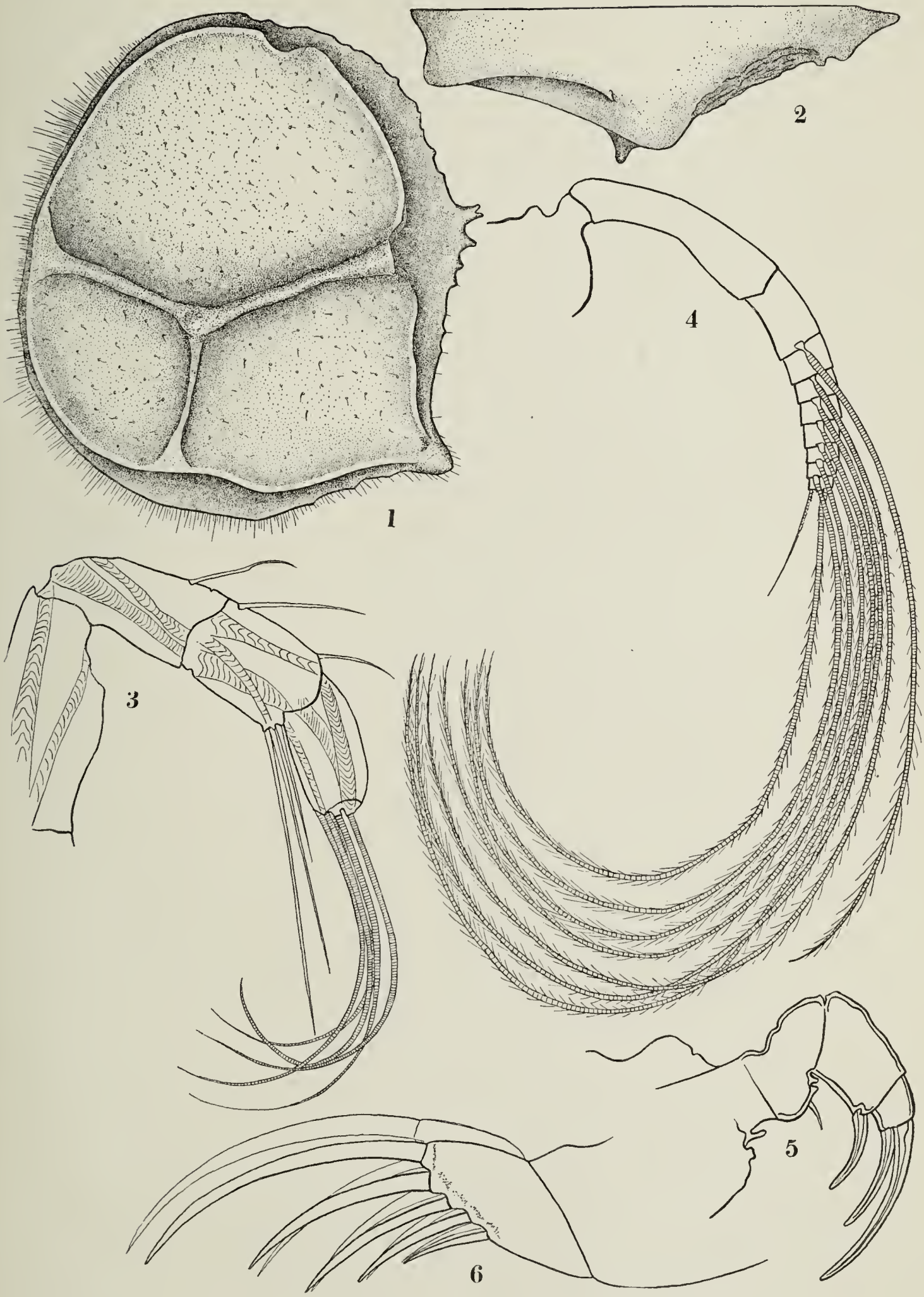

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PLATE 28.

Sarsiella zostericola sp. nov.

Fig. 7. Shell of male from side. × 35.
Fig. 8. Shell of male from above. × 35.
Fig. 9. Antennula of male. × 85.
Fig. 10. Antenna of male. × 85.
Fig. 11. Secondary branch of antenna of male. × 160.
Fig. 12. Mandibular foot of male. × 160.
Fig. 13. Abdominal lamina of male. × 85.
Fig. 14. Copulatory organ of male. × 160.
Fig. 15. Outline of shell of female from side. × 35.
Fig. 16. Antennula of female. × 160.
Fig. 17. Secondary branch of antenna of female. × 160.
Fig. 18. Mandibular foot of female. × 160.

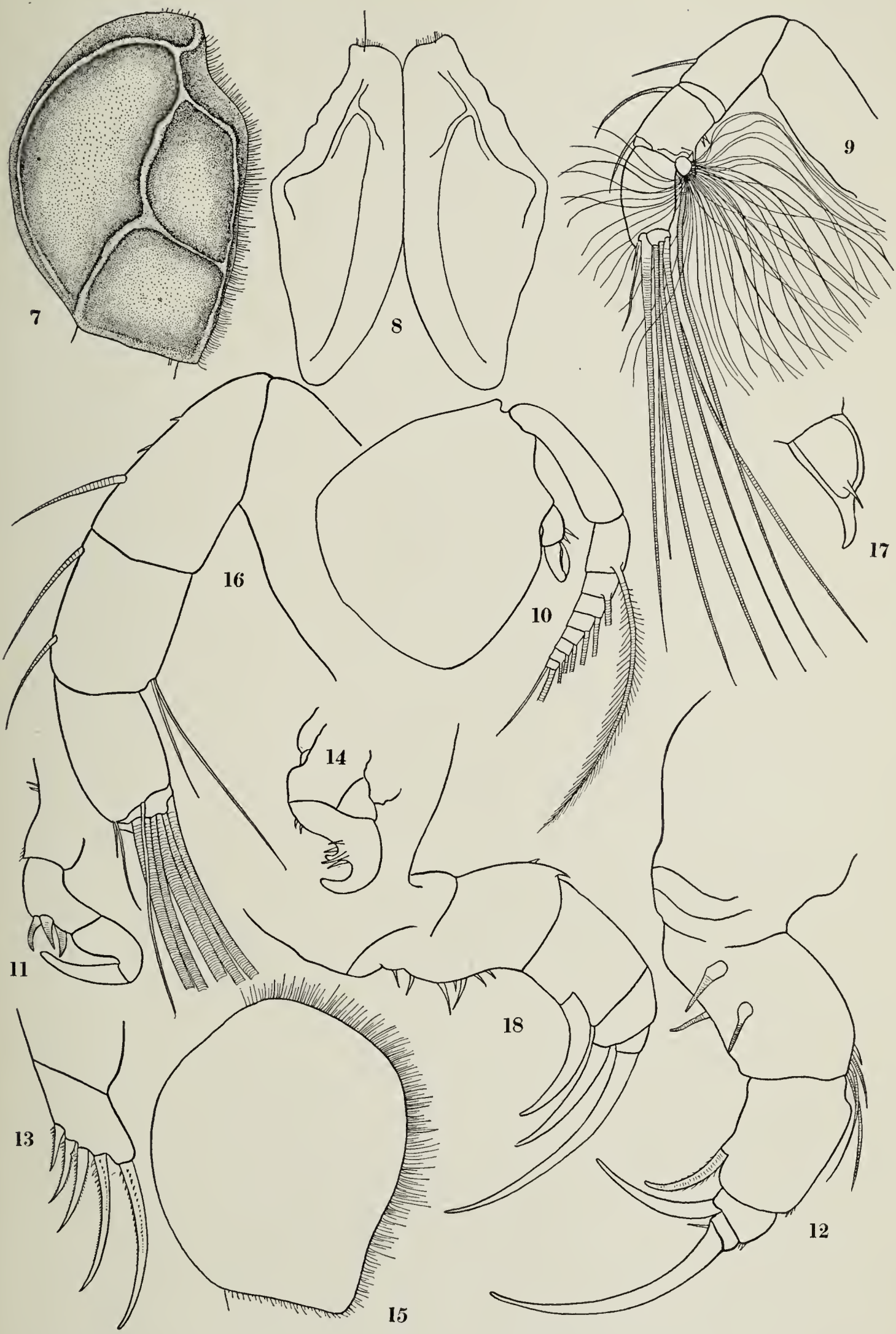

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PLATE 29.

Cylindroleberis mariae (Baird).

Fig. 19. Shell of male from side. × 40.
Fig. 20. Shell of male from below. × 40.
Fig. 21. Antennula of male (elongated terminal setae represented only in part). × 100.
Fig. 22. Antennula of female. × 100.
Fig. 23. Antenna of male (setae indicated only). × 100.
Fig. 24. Mandibular foot of female. × 175.
Fig. 25. Abdominal ramus of female. × 100.

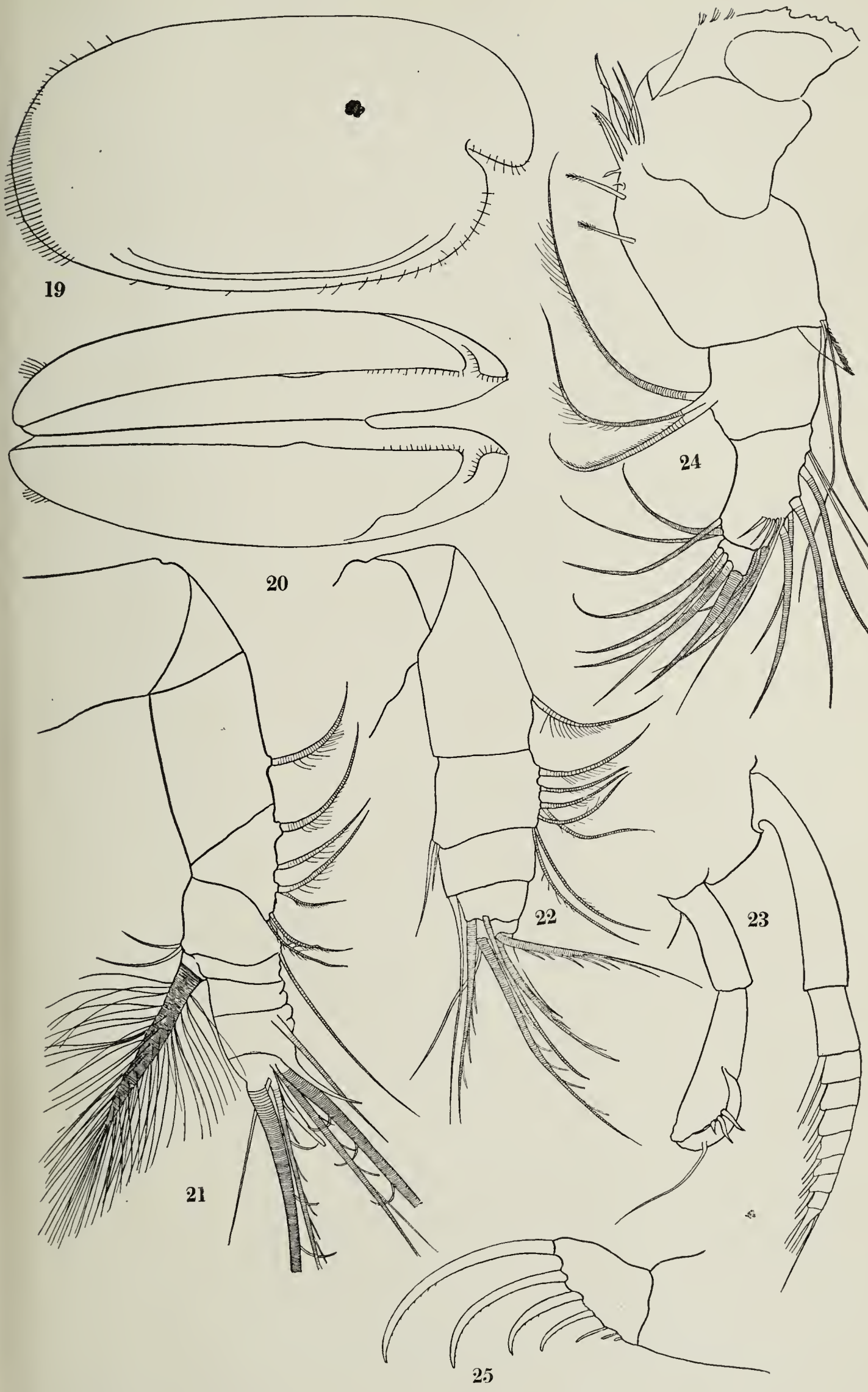

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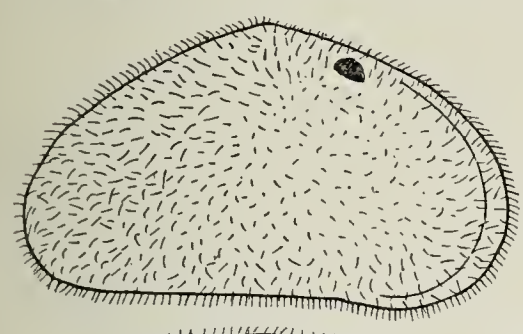
PLATE 30.

Pontocypris edwardsi sp. nov.

Fig. 26. Shell of female from side. × 60.
Fig. 27. Shell of female from below. × 60.
Fig. 28. Antennula of female. × 220.
Fig. 29. Antenna of female. × 220.
Fig. 30. Mandible of female. × 220.
Fig. 31. Maxilla and maxillary foot of female. × 220.
Fig. 32. Second foot of female. × 220.
Fig. 33. First foot of female. × 220.
Fig. 34. Abdominal ramus of female. × 220.



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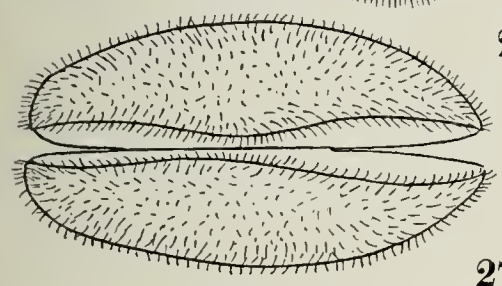

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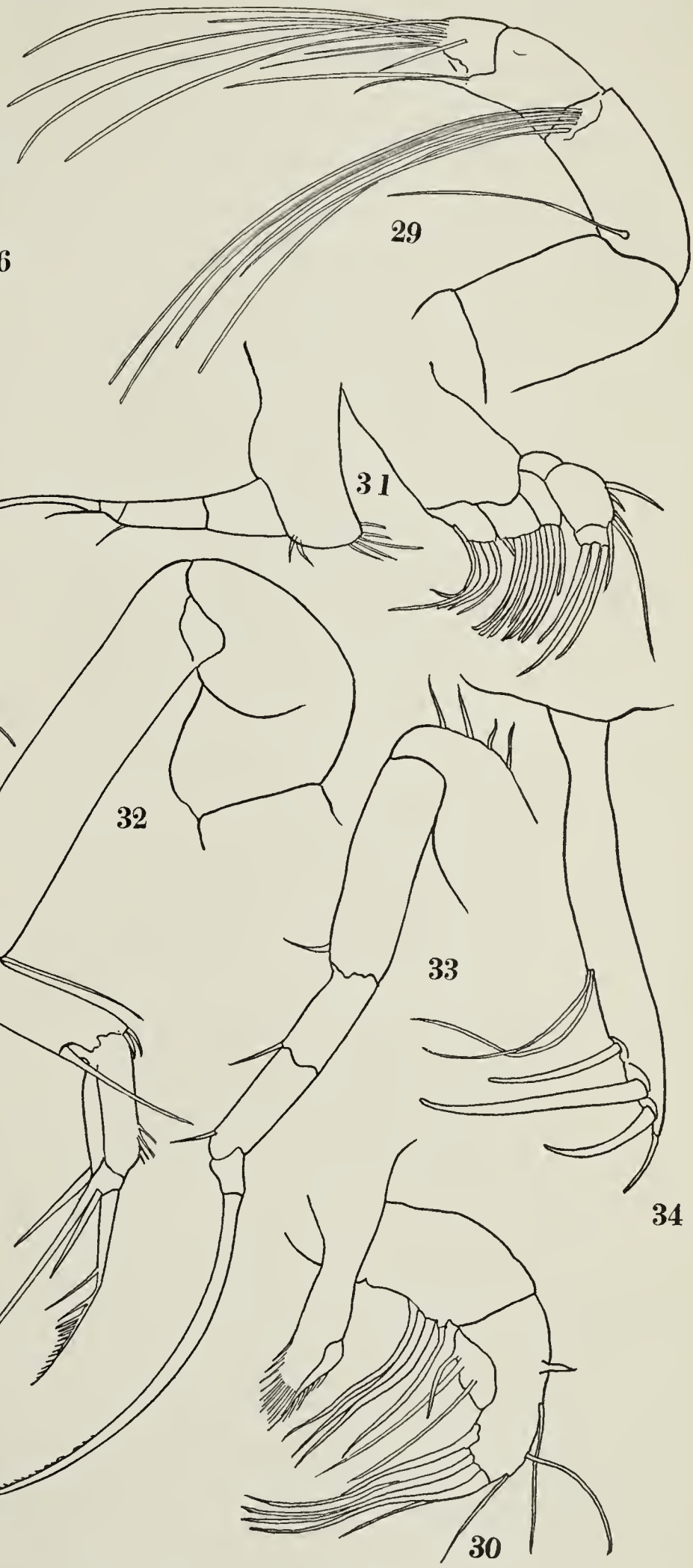

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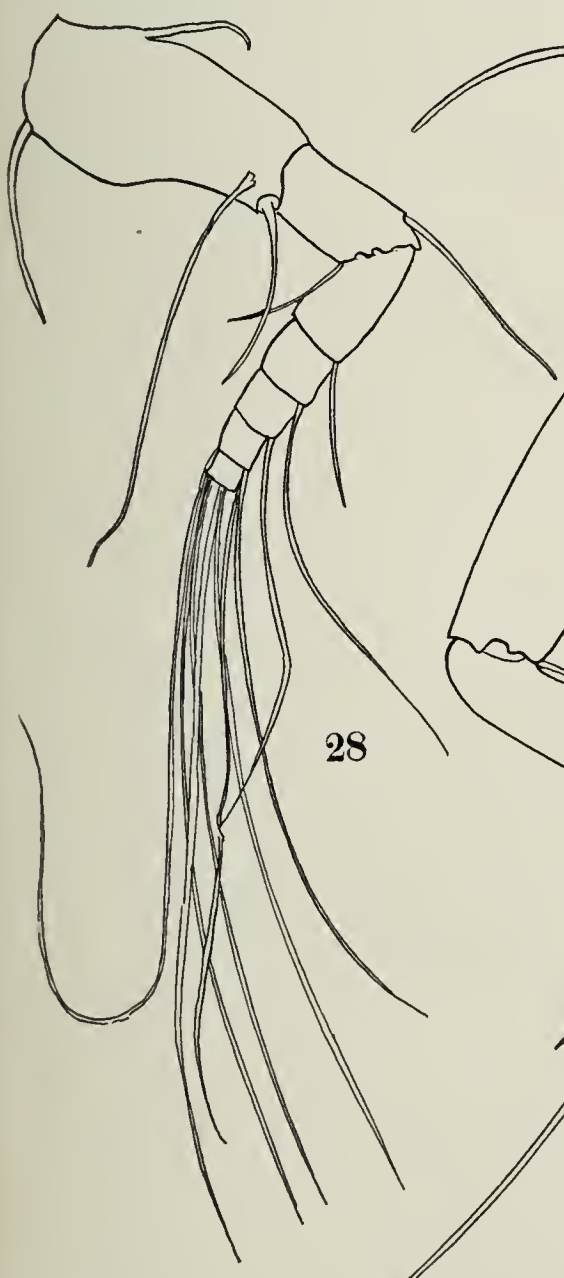

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PLATE 31.

Cytherois zostericola sp. nov.

Fig. 35. Shell of female from side. × 65.
Fig. 36. Shell of female from below. × 65.
Fig. 37. Antennula of female. × 275.
Fig. 38. Antenna of female. × 275.
Fig. 39. Mandible of female. × 275.
Fig. 40. Maxilla of female. × 275.
Fig. 41. Third foot of female. × 275.

Loxoconcha guttata (Norman).

Fig. 42. Shell from side. × 65.
Fig. 43. Antennula. × 150.
Fig. 44. Antenna. × 150.
Fig. 45. Maxilla. × 275.
Fig. 46. First foot. × 150.
Fig. 47. Second foot. × 150.
Fig. 48. Third foot. × 150.

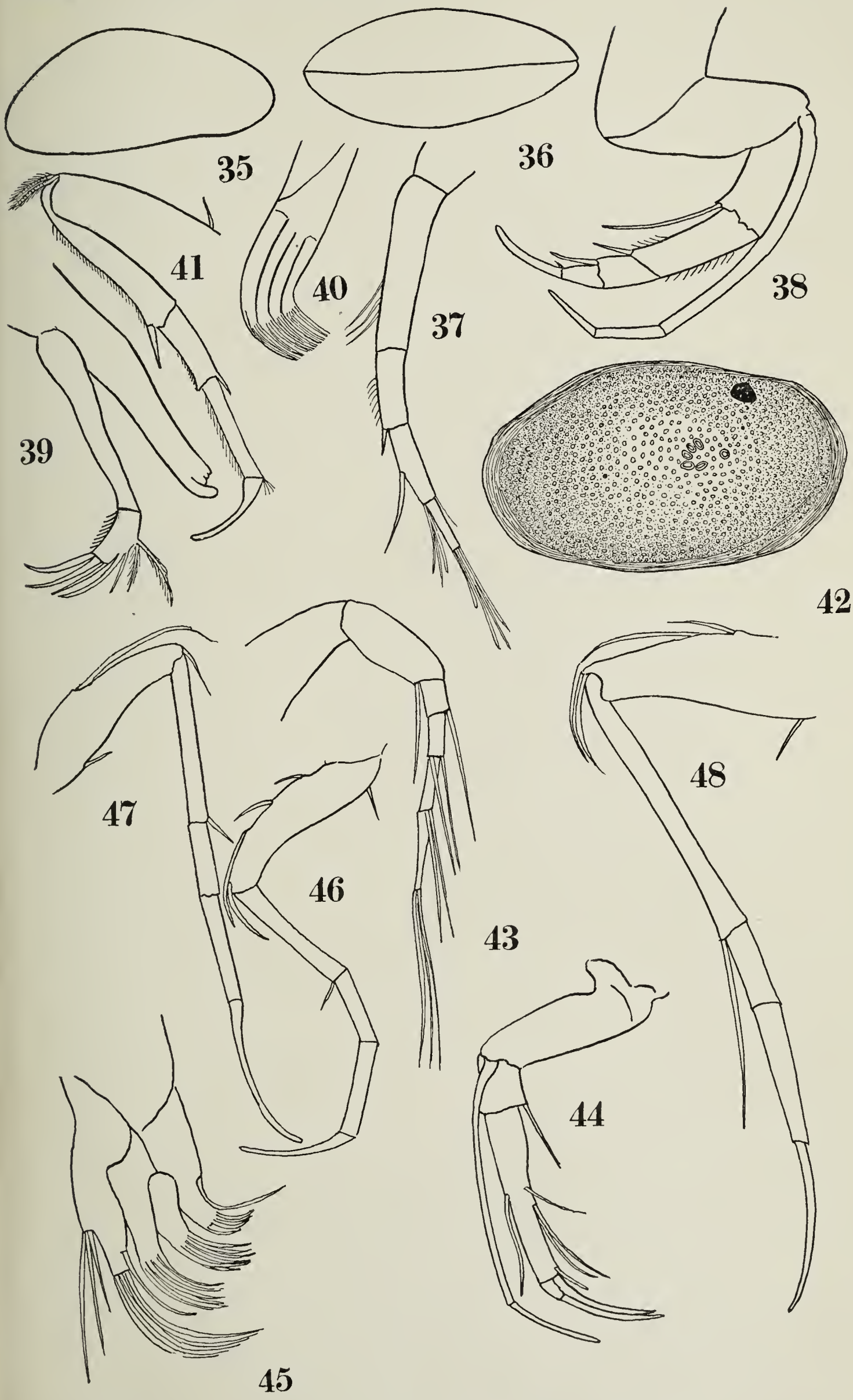

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PLATE 32.

Loxoconcha impressa (Baird).

Fig. 49. Shell of female from side. × 60.
Fig. 50. Shell of female from below. × 60.
Fig. 51. Antennula of female. × 220.
Fig. 52. Antenna of female. × 220.
Fig. 53. Mandible of female. × 220.
Fig. 54. Second foot of female. × 220.
Fig. 55. Third foot of female. × 220.

Loxoconcha guttata (Norman).

Fig. 56. Copulatory organ of male. × 220.

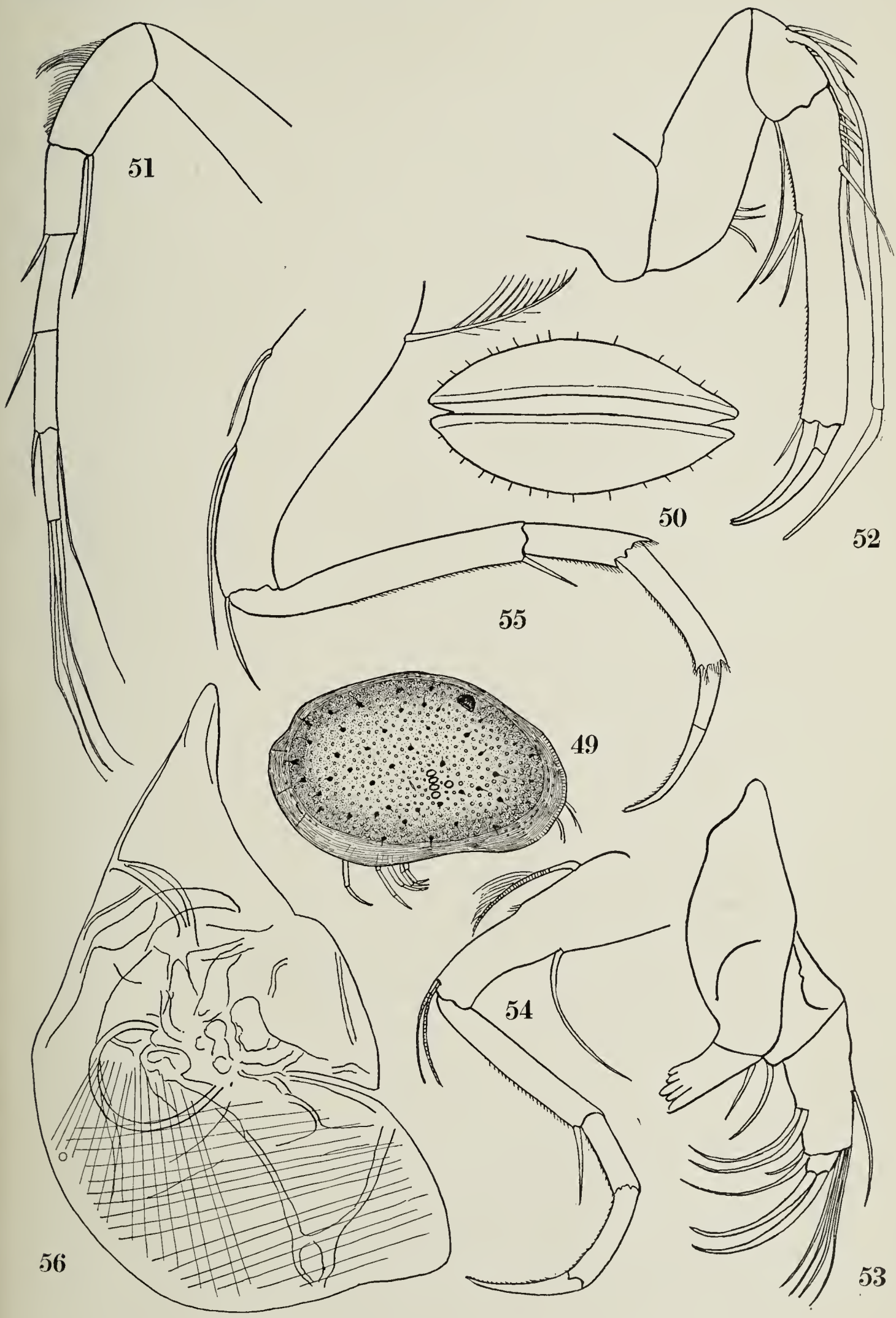

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PLATE 33.

Cytheridea rubra Müller.

Fig. 57. Shell of female from side. × 45.
Fig. 58. Shell of female from below. × 45.
Fig. 59. Antennula of female. × 210.
Fig. 60. Mandible of female. × 210.
Fig. 61. Second and third feet of female. × 210.

Cytheridea seminuda sp. nov.

Fig. 62. Shell of male from side. × 45.
Fig. 63. Antenna of male. × 210.
Fig. 64. Copulatory organ of male. × 120.

Cytheridea papillosa Bosquet.

Fig. 65. Shell from side. × 45.
Fig. 66. Shell from above. × 45.

Cytheridea americana sp. nov.

Fig. 67. Mandible of male. × 210.

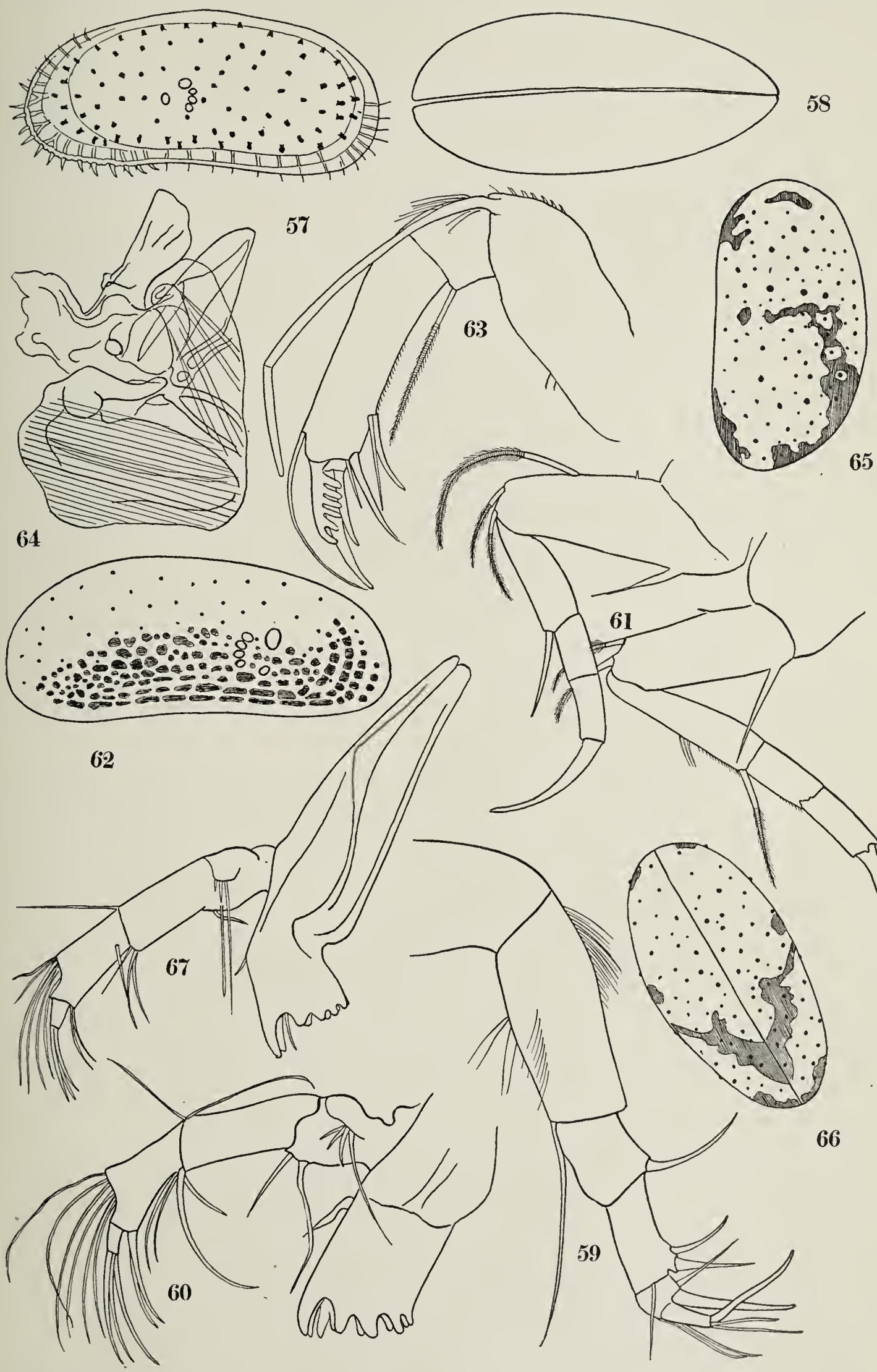

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PLATE 34.

Cytheridea americana sp. nov.

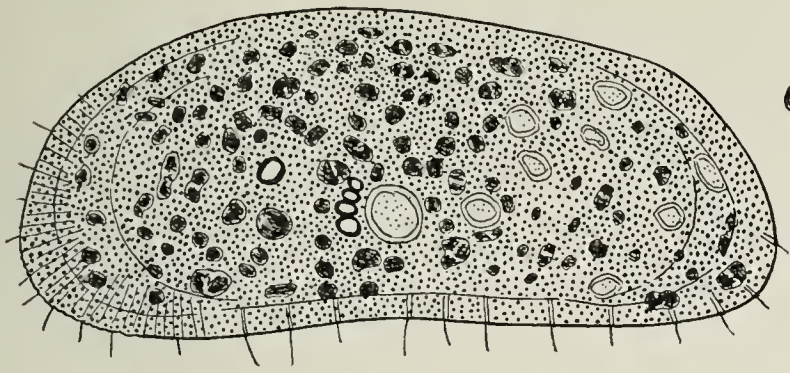
Fig. 68. Shell of male from side. × 65.
Fig. 69. Shell of male from above. × 65.
Fig. 70. Antennula of male. × 150.
Fig. 71. Antenna of male. × 150.
Fig. 72. Mandible of male. × 275.
Fig. 73. First foot of male. × 150.
Fig. 74. Second and third feet of male. × 150.
Fig. 75. Copulatory organ of male. × 150.

Cytheridea seminuda sp. nov.

Fig. 76. Second foot, left, of male. × 275.
Fig. 77. Second foot, right, of male. × 275.

Cytheridea rubra Müller.

Fig. 78. Antenna of female. × 150.



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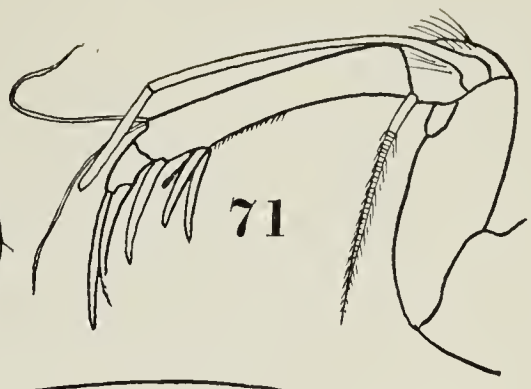

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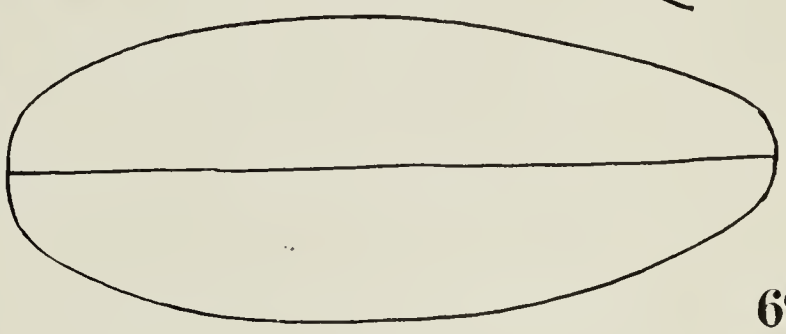

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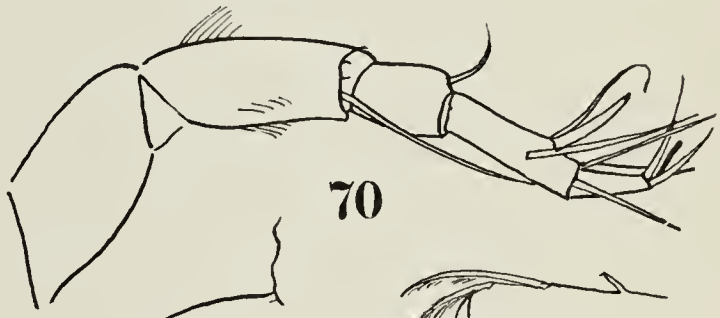

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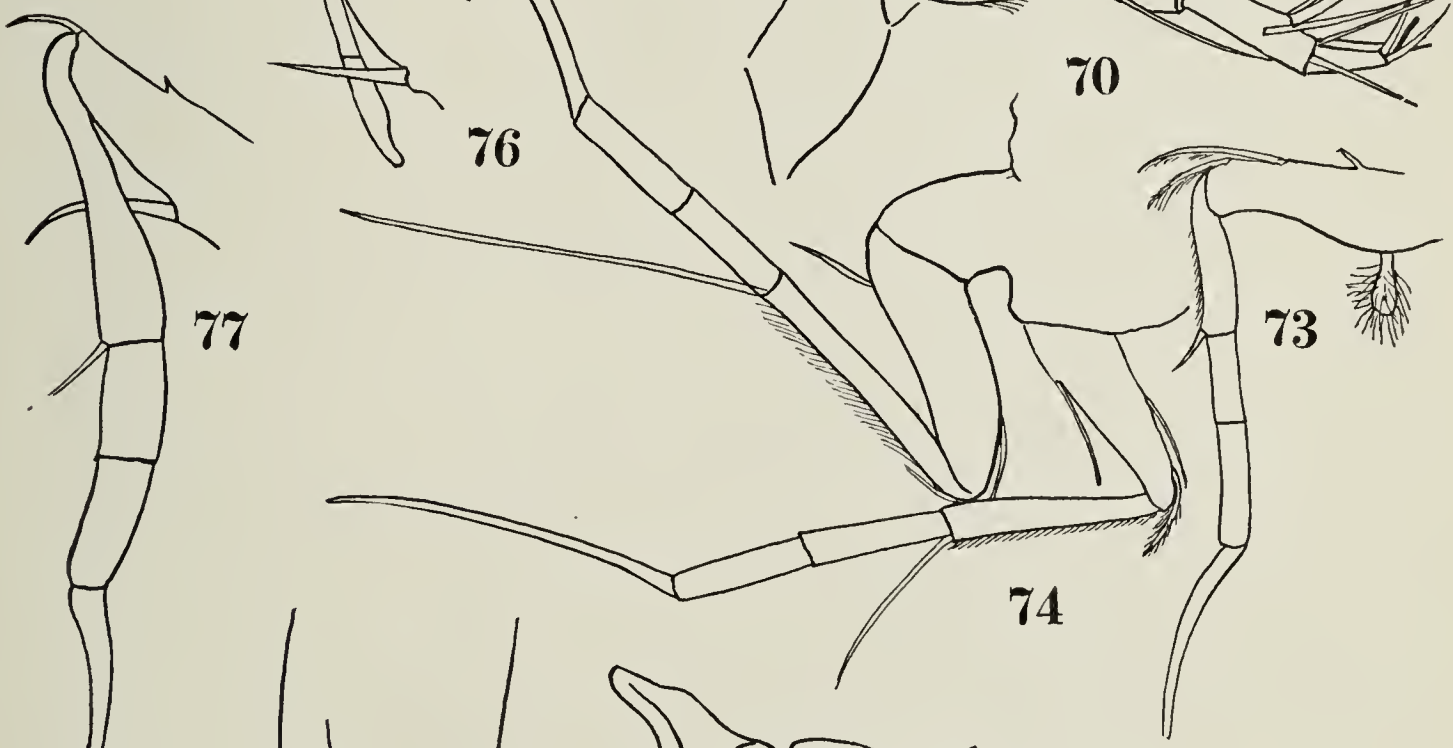

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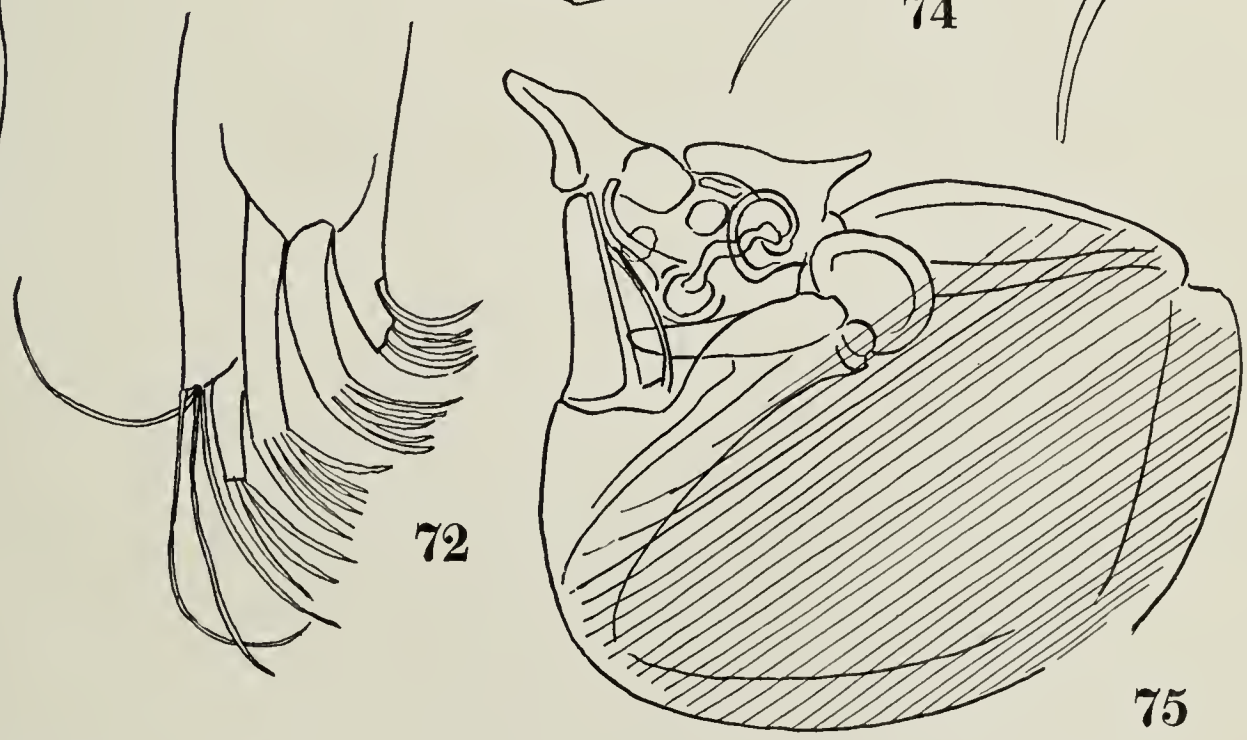

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PLATE 35.

Cythereis emarginata Sars.

Fig. 79. Shell from side. × 60.
Fig. 80. Antennula. × 220.
Fig. 81. Mandible. × 220.
Fig. 82. First foot. × 220.

Cythereis albomaculata (Baird).

Fig. 83. Shell from side. × 60.

Cythere dawsoni Brady.

Fig. 84. Shell from side. × 60.
Fig. 85. Shell from above. × 60.

Cythereis phalaropi sp. nov.

Fig. 86. Antennula of male. × 150.
Fig. 87. Antenna of male. × 150.
Fig. 88. Mandible of male. × 150.
Fig. 89. Maxilla of male. × 150.
Fig. 90. First foot, right, of male. × 150.
Fig. 91. First foot, left, of male. × 150.
Fig. 92. Second foot, right, of male. × 150.
Fig. 93. Second foot, left, of male. × 150.
Fig. 94. Third foot of male. × 150.

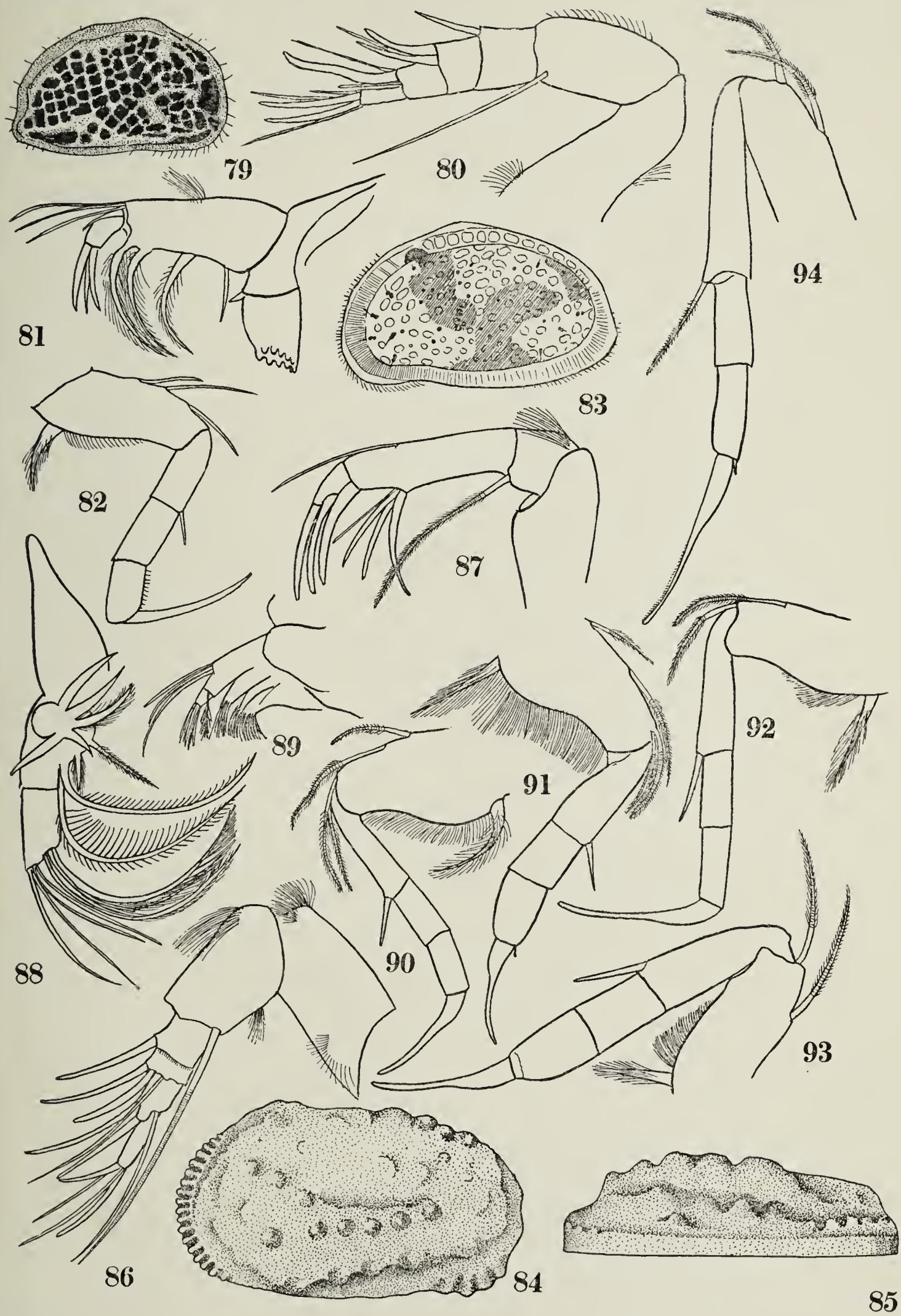

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PLATE 36.

Cythereis phalaropi sp. nov.

Fig. 95. Shell of male from side. × 40.
Fig. 96. Shell of male from below. × 40.

Cythereis arenicola sp. nov.

Fig. 97. Shell of male from side. × 40.
Fig. 98. Shell of male from below. × 40.
Fig. 99. Shell of male from within. × 40.
Fig. 100. One of the circular markings enlarged. × 150.
Fig. 101. Antennula of male. × 100.
Fig. 102. Antenna of male. × 100.
Fig. 102a. Mandible of male. × 100.
Fig. 103. Maxilla of male. × 100.
Fig. 104. First foot of male. × 100.
Fig. 105. Second foot of male. × 100.
Fig. 106. Third foot of male. × 100.
Fig. 107. Copulatory organ of male. × 185.

Cythereis tuberculata Sars.

Fig. 108. Antennula and antenna. × 185.
Fig. 109. Second foot. × 185.

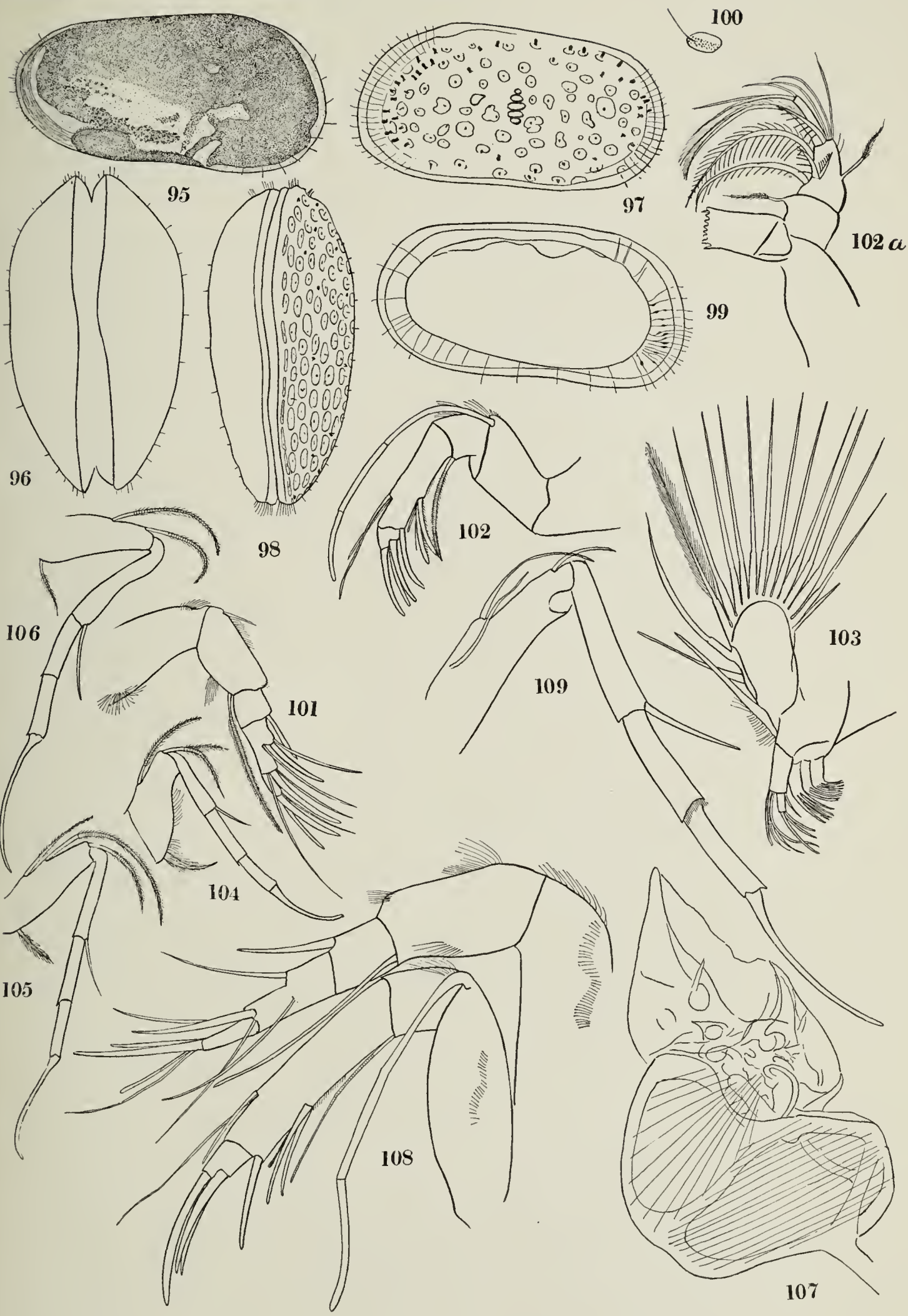

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PLATE 37.

Cythereis vineyardensis sp. nov.

Fig. 110. Shell of male from side. × 60.
Fig. 111. Shell of male from above. × 60.
Fig. 112. Antennula of male. × 220.
Fig. 113. First foot of male. × 220.
Fig. 114. Portion of third foot of male. × 220.

Cytherideis fasciata (Brady and Robertson).

Fig. 114a. Shell from side. × 60.
Fig. 115. Antennula. × 220.
Fig. 116. Antenna. × 220.
Fig. 117. Maxilla. × 220.
Fig. 118. First foot. × 220.

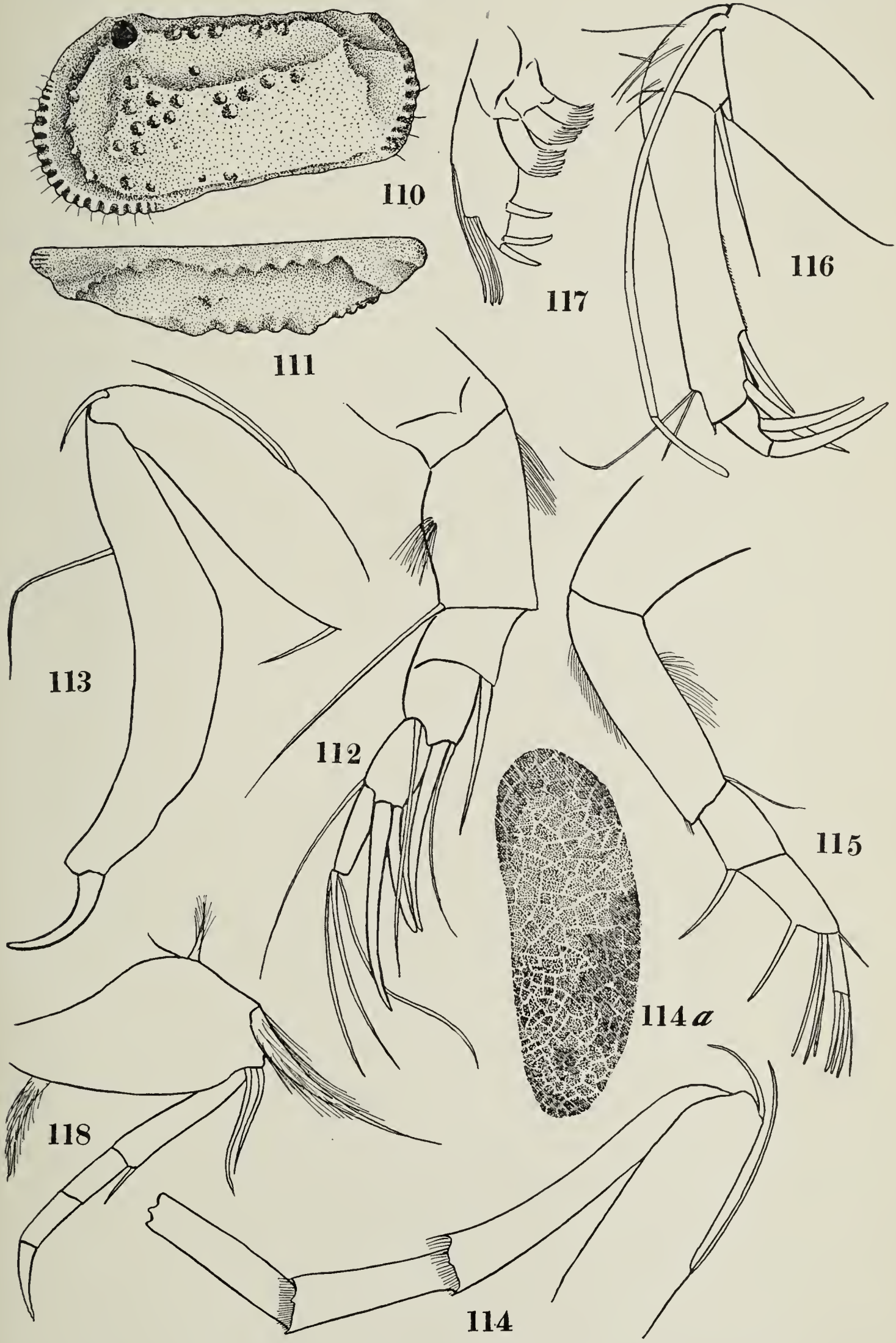

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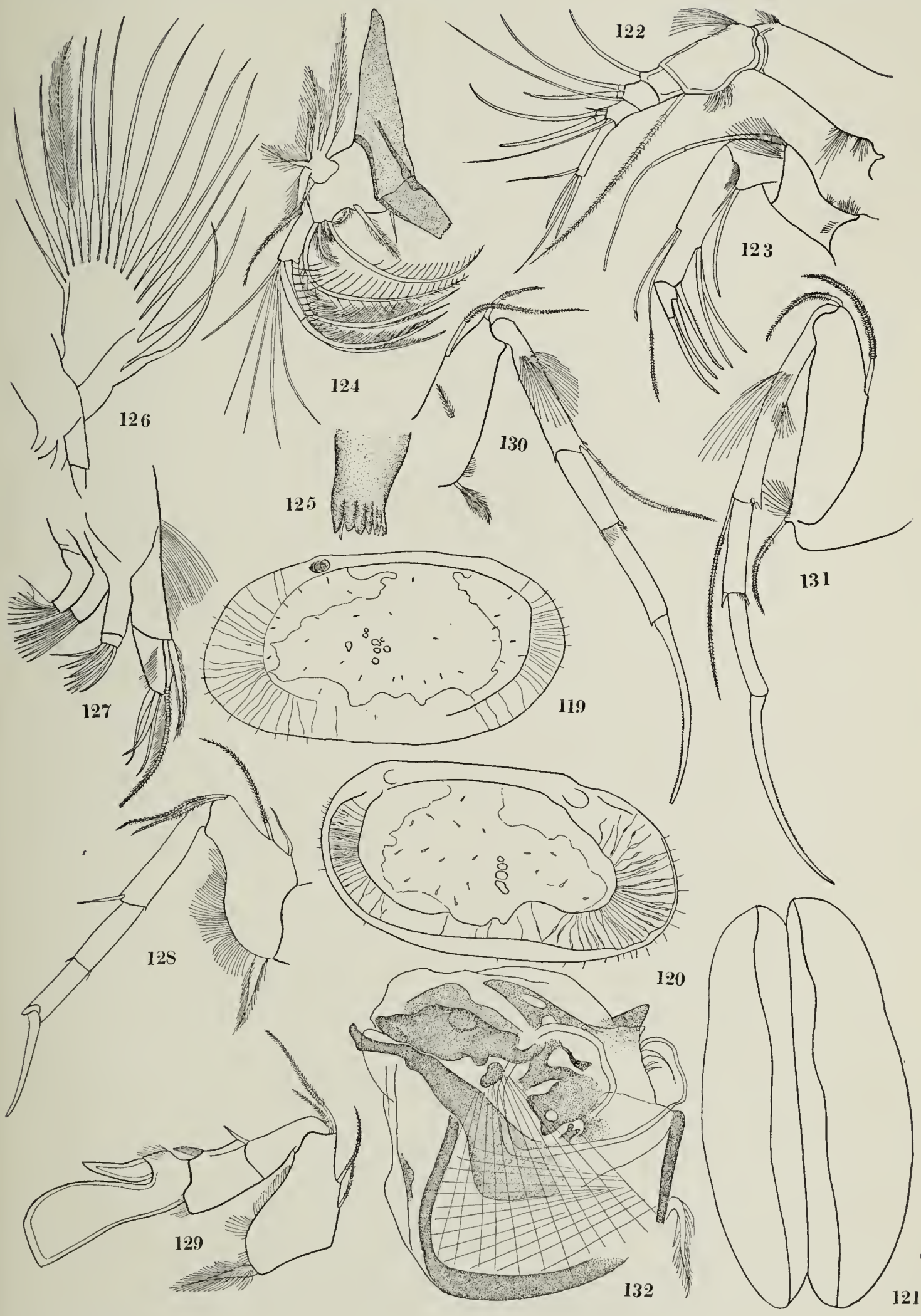
PLATE 38.

Pseudocytheretta edwardsi sp. nov.

Fig. 119. Shell of male from side. × 40.
Fig. 120. Shell of male from within. × 40.
Fig. 121. Shell of male from below. × 40.
Fig. 122. Antennula of male. × 100.
Fig. 123. Antenna of male. × 100.
Fig. 124. Mandible of male. × 100.
Fig. 125. Jaw of mandible. × 185.
Fig. 126. Maxilla of male. × 100.
Fig. 127. Palp of maxilla. × 185.
Fig. 128. First foot, left, of male. × 100.
Fig. 129. First foot, right, of male. × 100.
Fig. 130. Second foot of male. × 100.
Fig. 131. Third foot of male. × 100.
Fig. 132. Copulatory organ of male. × 100.



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SQUAMOSAL BONE IN TETRAPODOUS VERTEBRATA.

By F. W. Thyng.

BOSTON:

PRINTED FOR THE SOCIETY.

April, 1906.

No. 11.—SQUAMOSAL BONE IN TETRAPODOUS VERTEBRATA.[1]

BY F. W. THYNG.

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Introduction.

One of the most vexed questions of comparative osteology is that of the homologies of the squamosal bone throughout the vertebrates. Slight study of the literature shows that the name squamosal has been applied to several bones while the bone which, as I hope to show, is the homologue of the human squamosal, has had a number of names.

The term squamosal, including its various forms, was first applied to an element in the human skull which later fuses with others to form the temporal bone. Hence in applying the term to the lower groups the laws of nomenclature demand that it be given to that element alone which is the homologue of the squamosal in man. It is also evident that all possible criteria should be utilized in settling these homologies, not alone those of adult relationships and articulations but those of development as well.

The relations of the squamosal in the adult Mammalia differ slightly in the several orders, but nowhere is there the slightest doubt as to its homologies with the element in man. In general it may be defined as follows. It is a bony lamina usually sharing in the formation of the lateral wall of the brain case, but occasionally excluded therefrom when the periotic extends to the temporal. It articulates anteriorly with the alisphenoid, and sometimes with the frontal; dorsally with the parietal; posteriorly with the exoccipital and the mastoid portion of the petrosal; and ventrally with the tympanic and the petrosal. From its lower anterior angle it gives rise to a zygomatic process which articulates with the jugal (when present) and which bears on its ventral surface the glenoid fossa, bounded posteriorly in many forms by a well marked postglenoid process. This zygomatic process forms the external posterior border of the temporal vacuity. In man the squamosal is indistinguishably fused to the petrosal and

APR 26 1906

[1] Contributions from the Biological laboratories of Tufts college. No. XLIV.

tympanic bones to form the temporal bone but in some mammals the three remain distinct throughout life.

In the following *résumé* of previous work on the development of the squamosal in the Mammalia, no attempt has been made to obtain complete citation but only those articles are quoted which have been found to mark definite progress.

The earliest account of the development of the temporal bone which I have found is the excellent one of Kerckringius (**1670**). He apparently adopts the term squamosal from some earlier writer since he says: "Ossis temporum binas vulgo anatomici affignant partes, quarum unam os petrosum, alteram squamosum appellitant." He was well aware of the fact that many bones of the adult are formed by the fusion of distinct embryonic elements and he points out that the temporal bone arises by the fusion of (1) the annulus tympanicus, (2) the squamosum, and (3) the petrosum. He further recognizes the mastoid process as a part of the petrosum, in which he points out the existence of three ossificatory centers. He also called attention to the fact that the styloid process was preformed in cartilage and did not consider it a part of the temporal bone.

Meckel ('**15**–'**20**, p. 112) recognized four bony elements in the human temporal: (1) "das Felsentheil" (pars petrosa), (2) "das Zitzentheil" (pars mastoidea), (3) "das Schuppentheil" (pars squamosum), and (4) "der Trommelfellring" (annulus membrani tympani). But on a preceding page (107) of the same work he states that his "Zitzentheil" is only a part of the "Felsentheil." Hence he hardly differs from Kerckringius in his results.

Cuvier studied the squamosal from the comparative standpoint. Some of his results will be referred to later. Here it may be stated that, following Meckel he ('**25**) recognized the following elements in the human temporal: (1) "l'écailleuse et zygomatique," (2) "la tympanique," (3) "le rocher," (4) "la partie mastoïdienne." He, however, regarded the mastoid as a distinct element and as will be pointed out later, confused our nomenclature by recognizing, among the membrane bones of the lower vertebrates, distinct mastoids.

Hallmann's well known work ('**37**) on the temporal bone was likewise comparative, but while he added much to our knowledge of the non-mammalian forms he scarcely advanced beyond Meckel and Cuvier regarding the development.

Huxley ('**64**) gave a clear summary of existing knowledge of the

temporal and the substance of his account may be repeated here. The squamosal is developed in membrane upon the outer side of the periotic cartilage. It is, at first, a mere rod, the zygoma, with an expanded portion, the squama temporalis. Its lower edge is at first nearly straight but it soon develops a curved process (the margo tympanicus or posterior process of the adult human temporal) downwards behind the auditory meatus and between the tympanic ring and the periotic bones.

Development of the Squamosal in Mammals.

My studies of the development of the squamosal in the mammals are based upon serial sections and wax reconstructions of embryo pigs. In most respects my results are but confirmations of the accounts of others, but they show certain points which have not been sufficiently valued or which have been overlooked by others, and which, it seems to me, have great importance in determining the homologies of this bone in other groups.

The squamosal (pl. 39, fig. 1, *Sq.*) arises as a membrane bone, consisting of a zygomatic process in front and a small squamous portion behind. The zygomatic process articulates anteriorly with a simultaneously developed jugal or malar (*J.*) while the upper part of the squamous portion overlies the lateral border of the cartilaginous otic capsule directly in front of the ampullar ends of the anterior and the horizontal (external) semicircular canals. Its lower half extends ventrally as a slender splint (the margo tympanicus of Henle) down below the capsule and over the processus brevis of the incus. This portion deserves especial attention since there seems to be an intimate relation between this margo tympanicus and the incudal element. As shown in figures 2 (pl. 39) and 3 (pl. 40) representing sections of a pig of 72 mm. total length, a dense and fibrous stroma unites the squamosal with the incus. This condition, which has been overlooked by previous writers, I regard as very important as indicating a close primitive relation between incus and squamosal to which reference will be made again later.

Another important morphological character which deserves special emphasis is that, in its early development, the squamosal is widely separated from the parietal, for there is a wide gap between the dorsal

margin of the squamosal and the lateral margin of the parietal, (pl. 39, figs. 1, 2, *Sq.* and *Pa.*) This is shown in the figures of numerous works, (*e. g.*, Huxley, '64, fig. 61 B; Parker, '85, pl. 2, fig. 3; van Bemmelen, : 01, p. 770, pl. 30, fig. 5, pl. 31, fig. 5; Fischer, : 01, pl. 29, fig. 3; van Kampen, : 05, fig. 1; Gaupp, : 05, p. 844, fig. 406, etc.). On the other hand the close association of parietal and squamosal in the adult has led to what I regard as erroneous views of its homologies in the non-mammalian vertebrates. It is, however, sufficient to say at this point, that there is nothing in the early development which necessitates the identification of the mammalian squamosal with the bone which joins the parietal in the lower tetrapodous Vertebrata (Stegocephala and Cotylosauria).

The relation of the squamosal to the incus is, in my estimation, much more important. The conditions described indicate an intimate relation between the two elements in question in the ancestors of the Mammalia which has been lost in the latter group. This involves a discussion of the homologue or homologues of the incus in the non-mammalian vertebrates.

Three widely different views have been advanced upon this point, besides some minor variations such as that of Drüner (: 04) which scarcely demand attention since they do not affect the main questions at issue. These views are:—

1. The incus is the homologue of the hyomandibular.
2. The incus is a part of the Sauropsidan columella.
3. The incus is the quadrate, changed in form and function.

I am well aware that this is a much disputed question and that each of the three views has been advocated by able authorities. The whole matter has been reviewed recently by Gaupp ('99) and Kingsley (: 00) so that a summary of their results and references to more recent literature are all that is necessary here. It is indeed hardly necessary to deal with the arguments, *pro* and *con*, regarding the homologies indicated under 1 and 2 for, if it be shown that the third is correct, the others certainly cannot be true. The arguments concerning the third are as follows:—

1. The incus arises from the procartilage of the mandibular (pterygoquadrate-Meckelian) arch; so does the quadrate.
2. It arises in front of the Eustachian (spiracular) cleft; so does the quadrate. The columella and the hyomandibula, on the other hand, are postspiracular.

3. Its relations to the chorda tympani are those of the quadrate, and negative the view that it can be either a part of the Sauropsidan columella or the hyomandibula of lower vertebrates.

4. Its articulation with the malleus is of the same kind as that most common between the quadrate and the articulare in the non-mammalian vertebrates.

The only important papers dealing with these homologies since that of Kingsley are those of Gadow (: **01a**) and Broom (: **01**; : **04**). Gadow believes that the quadrate of the lower vertebrates is transformed into the tympanic of the mammals, a view for which he advances no adequate evidence and which is open to many insuperable objections. Gadow also tries to overthrow the arguments of Kingsley and Gaupp, derived from the relative position of bones, gill clefts, and nerves by supposing that these may shift so that an element which is behind a gill cleft in one group may be homologous with one lying in front of the same cleft in another, and that nerves may slip around the various arches in a similar manner. Reply to such views is scarcely possible; reference may be made to Broman (**'99**, p. 650).

Broom regards the quadrate as being transformed into the inter-articular cartilage found in the glenoid fossa of many mammals but the development of this is such as to preclude any such view, while the arguments as summarized by Kingsley and Gaupp for the incudo-quadrate homology render Broom's interpretation extremely improbable.

If, then, the incus be the homologue of the quadrate (and until more convincing adverse evidence than that already at hand is presented, most morphologists will continue so to regard it) it follows that association with the quadrate and otic capsule rather than juxtaposition with the parietal will be the most weighty evidence in ascertaining the homologue of the squamosal in the non-mammalian vertebrates.

Cuvier carried his homologies into the lower vertebrates by way of the crocodiles, turtles, and lizards, and thence to the lower forms; and his conclusions have doubtless had great weight with all who have followed him. But this line is apt to lead (indeed has led) to erroneous conclusions. It would rather seem that we should follow the lines of descent.

According to all who have dealt with the subject of mammalian ancestry, this group has descended from either the reptilian group

Theromorpha or the Amphibian group Stegocephala, the differences between certain members of the two being very slight. It is, of course, impossible to study the development of the bones in either of these groups and even the relations of the chondrocranium and visceral arches to the covering bones are hardly known in either. Hence any light which may be thrown upon the subject by the nearest living forms must have some value. The nearest relatives of the Stegocephala are the Caecilians and the Urodeles, the Urodeles being in many respects admittedly degenerate and aberrant, while the Caecilians, as shown by many skeletal features, are decidedly the most Stegocephalian of all living Amphibia. Unfortunately the Caecilians, as will be detailed later, lack completely any element which can be homologized with the mammalian squamosal.

The Squamosal in Urodeles.

I have studied the development of the squamosal region in both Amblystoma and Amphiuma. In Amphiuma two bones are intimately related to the quadrate in development, one more external and more dorsal in position, the other more ventral and resting directly upon the quadrate. The latter will be considered later. The external and more dorsal bone (pl. 40, fig. 4), is membranous in origin. It overlies the upper external surface of the quadrate (*Qu.*) and extends thence upward upon the lower part of the otic capsule, overlying the external (horizontal) semicircular canal. In its early stages it is separated by a wide interval from the lateral margin of the parietal (*Pa.*). (*Cf.* Kingsley, '99, p. 165, fig. 144.) In other words, accepting the homology between incus and quadrate, this bone corresponds perfectly in position and relations to the mammalian squamosal with the single exception that, since no jugal is developed in the Urodeles, it lacks the jugal-squamosal articulation.

This bone in the Urodelan skull has had numerous names proposed for it. It has been called the tympanique or tympanicum (Cuvier, Stannius, '56, Wiedersheim, '77, Gegenbaur, '78, Hoffmann, etc.); a portion of the quadrate (os carré, Hallmann, Meckel); the temporomastoïdien (Dugès); the paraquadrate (Gaupp, Emerson, etc.) and the squamosal (Cope, Hasse, Huxley, '74, Parker, Hay, '90, Wiedersheim, '93, Gegenbaur, '98, Kingsbury, Gadow, and others). The term tympanic cannot be applied to it since it is already in use for the

bone supporting the tympanic membrane of the mammals (pl. 39, fig. 1, *Ty.*) which is clearly without homology with this element.

Gaupp ('94) studying the hammer-shaped bone in the temporal region of the Anuran skull found that it arose as a membrane bone primitively related to the quadrate and only secondarily extending upon the otic capsule (thus confirming Gegenbaur, '78, p. 481). He therefore called it the 'paraquadrate' a name which he suggested might eventually be replaced by the term 'tympanicum.' From the Anura he proceeded to the Urodeles and concluded that the same conditions prevailed for the bone which there covers the external surface of the quadrate. He therefore concluded that neither of these Amphibian bones was homologous with the mammalian squamosal, since according to the information then available, the squamosal developed upon the otic capsule and was 'parotic' in character. While this condition may be true for the very specialized group of Anura it certainly does not hold for the Urodeles since there the element in question develops partly upon the otic capsule and partly upon the quadrate cartilage (*cf.* Kingsbury, :03, p. 314). Besides, contrary to Gaupp, (if we accept the incus=quadrate homology), this element corresponds exactly with the mammalian squamosal, hence Gaupp's term 'paraquadrate' is merely a synonym of squamosal, so far as the Anura and Urodela are concerned, and is unnecessary.

The Temporal Region in Caecilians.

I have studied the development of the skull in Ichthyophis and figure A shows the relations as they exist in the larval stage. It is at once evident that the area of the otic capsule which in Amphiuma is covered by the dorsal portion of the squamosal (pl. 40, fig. 4) is entirely without covering bones in the Caecilian. Further, as pointed out by Winslow ('98, p. 178) and Peter ('98) the otic process of the quadrate has disappeared, and there is certainly no bone which covers what may be considered as the external surface of the body of the quadrate, nor does one appear in later or in the adult stages. Hence it follows that, at least in Ichthyophis a true squamosal is lacking.

There is, however, a membrane bone present (*Pf.*) which develops over the postero-lateral edge of the parietal, the anterior dorsal part of the otic capsule, the adjacent dorsal portion of the trabecula, and

the external surface of the ascending process (*a. p.*) of the quadrate. This bone was known to Cuvier ('17, p. 87) as the 'temporal.' Dugès ('35) called it the jugal and in this has been followed by the cousins Sarasin ('90). Stannius ('56) called it the squama temporalis, Wiedersheim ('79) the squamosum, and Cope ('89) the squamosal. Huxley ('71) regarded it as the squamosal plus the quadratojugal of the Anura, while Gaupp ('94) thought that probably it corresponded to his paraquadrate and in this conclusion he has been followed by Peter ('98).

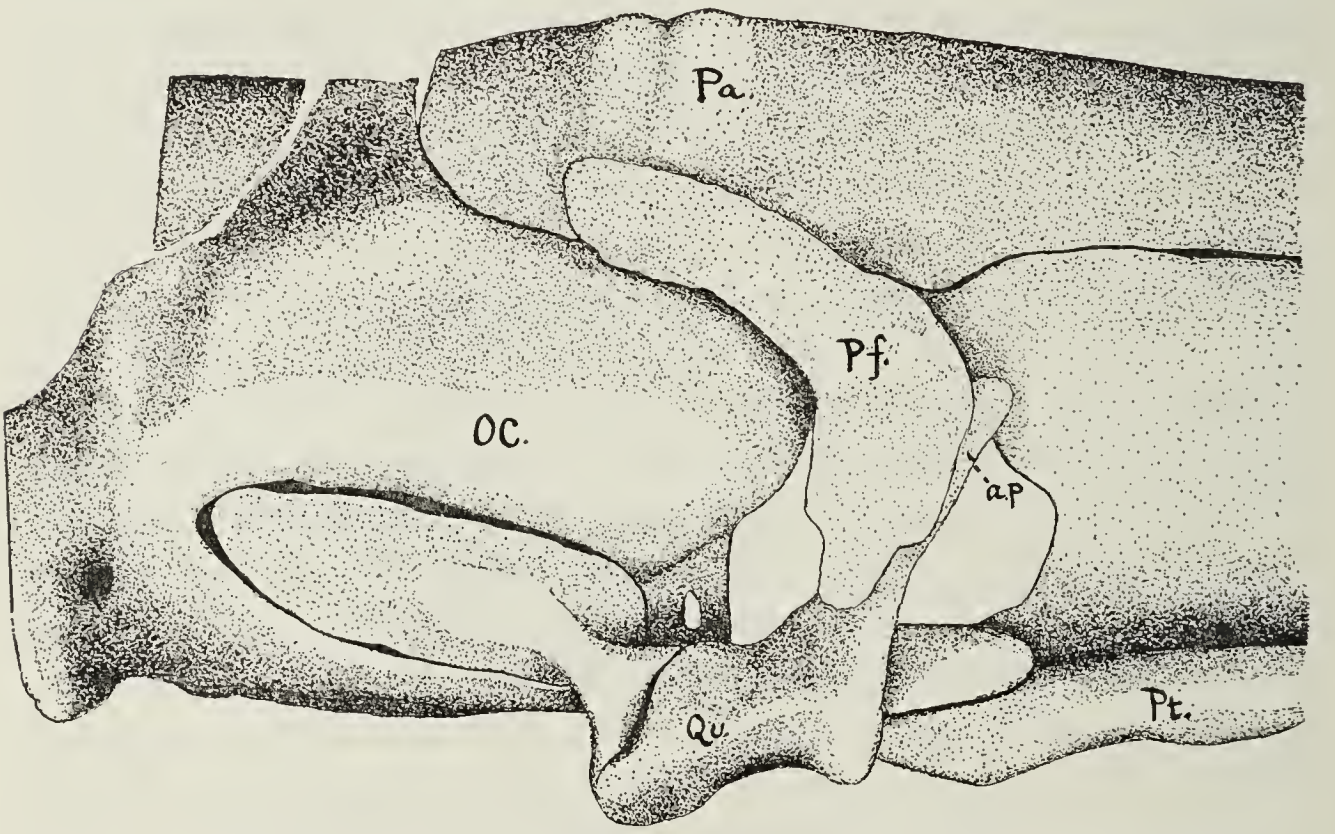

FIG. A. — Reconstruction of the temporal region of the skull in Ichthyophis (larval stage). *a.p.*, ascending process of quadrate; *OC.*, otic capsule; *Pa.*, parietal; *Pf.*, postfrontal; *Pt.*, pterygoid; *Qu.*, quadrate.

Gegenbaur ('98, p. 377, fig. 232) homologized it with the quadratojugal.

As already pointed out, its position in the larva does not warrant its consideration as the squamosal. Its identification as jugal or quadrato-jugal is negatived by its early history and relationships, while the fact that in the adult it articulates with the maxillary is apparently, as maintained by Peter ('98, p. 594), a secondary condition. As pointed out above, Gaupp's paraquadrate is merely a synonym of squamosal.

What, then, is the homology of this bone? The postfrontal suggests itself, especially when it is found that this bone in the embryo

lizard (*cf.* Gaupp, '94, fig. 9) has relations to the parietal, otic capsule, and columella (=epipterygoid= ascending process of the quadrate) which are extremely similar to those described above for the bone in question in Ichthyophis. It should be recalled that Wiedersheim ('79, p. 21) suggested that possibly this bone might be "ein weit ausgewachsenes hinteres Stirnbein."

It will be remembered that the Sarasins have already recognized a postfrontal in the bone which nearly surrounds the orbit and which by various authors has been regarded as a postorbital, a sclerotic, or a supraorbital. In the light of its relations as described above, the 'jugal' of the Sarasins corresponds more nearly to a postfrontal than does this osseous ring, which is therefore some other element. The Sarasins point out that the ring is not connected with the eyeball and hence cannot be a sclerotic, while its relations to postfrontal and frontal seem to negative its being a postorbital. Until further evidence is presented I am therefore inclined to call it a supra-orbital.

From the foregoing it would appear that no squamosal is found in the Caecilians and therefore our determination of the squamosal must depend upon comparisons with the Urodele skull, the nearest of all living forms to the Stegocephala.

Temporal Region in Stegocephala.

In the Urodeles but a single bone occurs between the parietal and the quadrate, but in the Stegocephala (figs. B and C) two bones usually intervene. The homology of the parietals in the two groups cannot be doubted, but beyond this there is an element of uncertainty. Lateral to the parietal there is a bone (*St.*, occasionally two as in Melanerpeton and Discosaurus) bounded anteriorly by the postfrontal (*Pf.*) and postorbital (*Po.*), laterally by a bone (*Sq.*) to be considered immediately, and posteriorly by the so called epiotic (*Ep.*) and supraoccipital (*So.*) plates. This bone is usually called the squamosal (Huxley, Miall, Fritsch, Credner, Fraas, Zittel, Baur, '94, Gaupp, Woodward, Gadow, Williston, etc.) but it has received various other names — Schuppenschläfenbein (Burmeister), supramastoid (Cope), supratemporal (Baur, '86, Ammon, Boulenger, and Broili). It overlies the otic capsule and has no connection with either quadrate or jugal and hence cannot be termed the squamosal according to the

previous definition of that element. I have called it the supratemporal for reasons which will appear later.

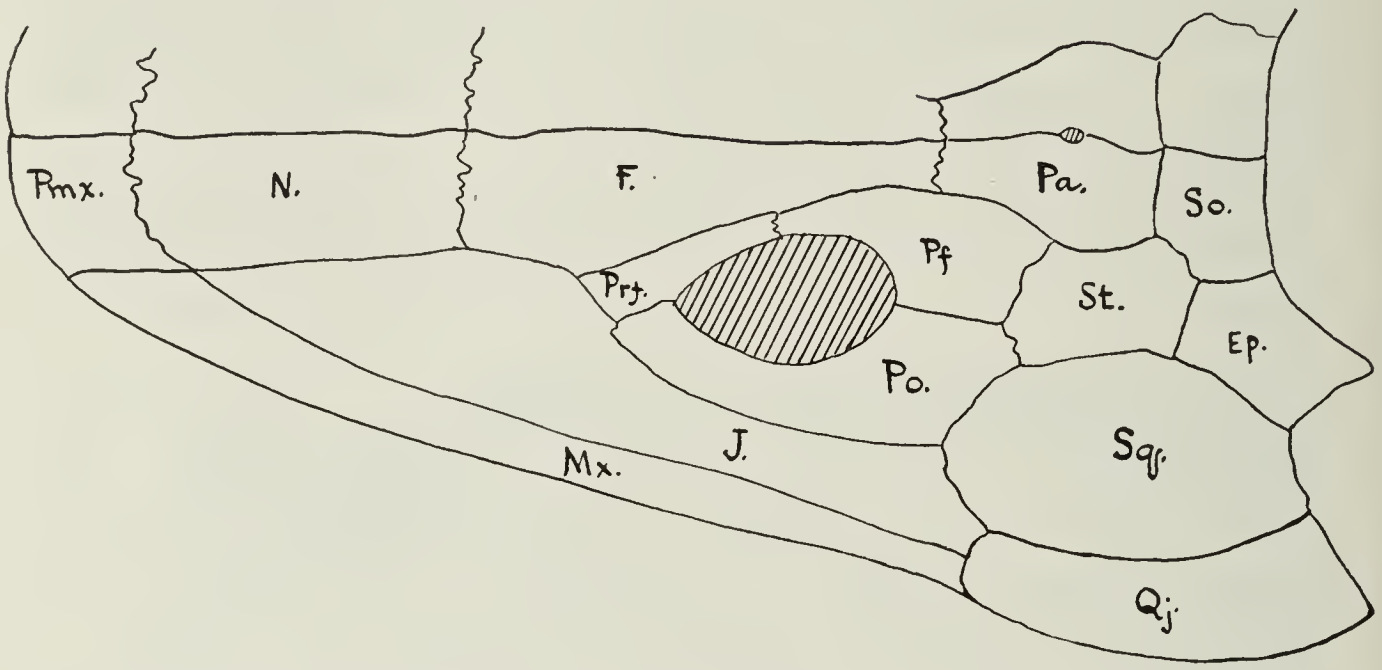

FIG. B. — Restoration of the skull of *Chelidosaurus uranyi* from Zittel, after Fritsch. *Ep.*, epiotic plate; *F.*, frontal; *J.*, jugal; *Mx.*, maxillary; *N.*, nasal; *Pa.*, parietal; *Pf.*, postfrontal; *Pmx.*, premaxillary; *Po.*, postorbital; *Prf.*, prefrontal; *Qj.*, quadratojugal; *So.*, supra-occipital plate; *Sq.*, squamosal; *St.*, supratemporal.

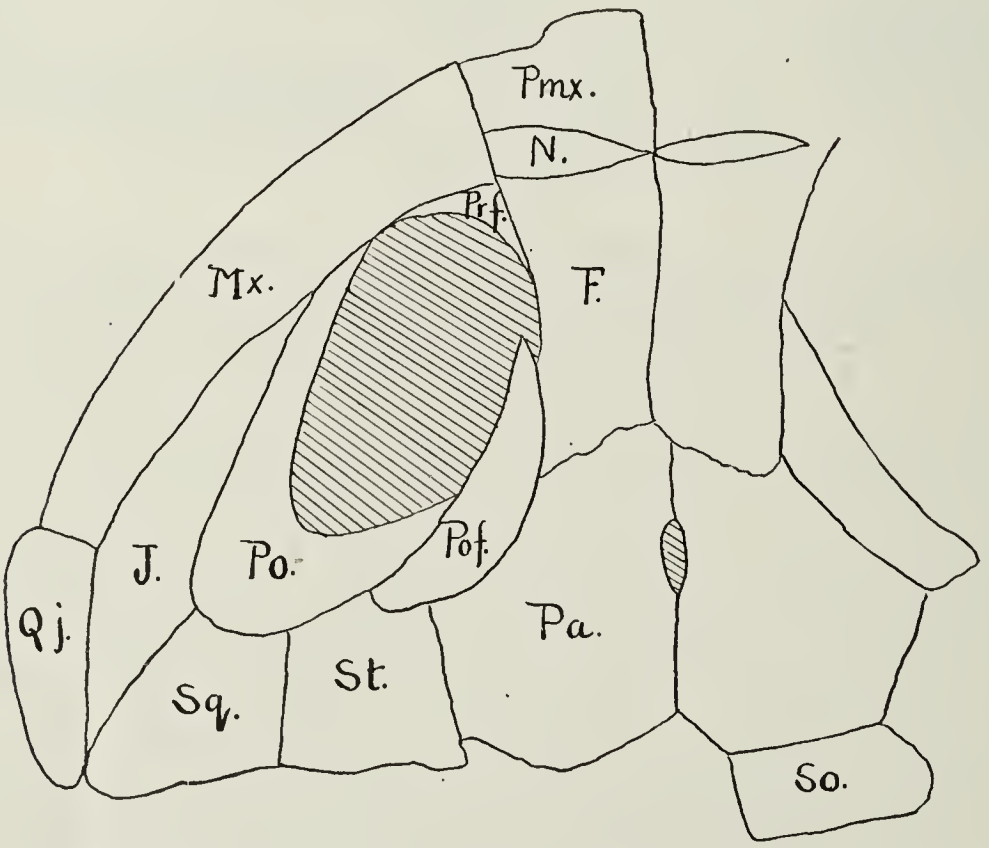

FIG. C. — Restoration of the skull of *Branchiosaurus gracilis*, after Credner. *F.*, frontal; *J.*, jugal; *Mx.*, maxillary; *N.*, nasal; *Pa.*, parietal; *Pmx.*, premaxillary; *Po.*, postorbital; *Pof.*, postfrontal; *Prf.*, prefrontal; *Qj.*, quadratojugal; *So.*, supra-occipital plate; *Sq.*, squamosal; *St.*, supratemporal.

Lateral to this supratemporal is a second element (*Sq.*) the supratemporal of Huxley, Miall, Fritsch, and the others cited above, but it has also received other names. It is the 'äusseres Paukenbein' of Burmeister, squamosal of Baur ('86), Ammon, Boulenger, and Broili, the prosquamosal of Baur ('94), Williston, and others, and the paraquadrate of Gaupp. It articulates anteriorly with the postorbital (*Po.*) and the jugal (*J.*), medially with the supratemporal, and laterally with the quadratojugal (*Qj.*). Although we have little evidence of internal structures, its position is such that it must overlie the lateral portion of the otic capsule and the quadrate, the latter a structure in Trematosaurus, according to Burmeister ('49, p. 28–29) very similar to that of the Crocodilia. Since, then, this bone agrees in its position and in its relation to quadrate and otic capsule with the squamosal of the Urodeles and with the same element in the mammals in these respects, as well as in its articulation with the jugal, it follows that it must be called the squamosal and that the terms supratemporal and squamosal as usually applied to the Stegocephala and their allies must be transposed. The more lateral bone is the squamosal, the more medial the supratemporal which in recent Amphibia has disappeared entirely (or has possibly fused with the parietal) thus accounting for the large interval between the parietal and the squamosal in the embryos of both Amphibia and Mammalia.

Now if this view be true that the supratemporal has disappeared in the Amphibia, Mammalia, and some other groups, we might expect that the supratemporal would show signs of reduction in some of the Stegocephala correlated with a corresponding increase of size in the squamosal. This is actually the case in many of the Stegocephala, as for instance the genera Pelosaurus, Melanerpeton, Archegosaurus, Chelidosaurus, Nyrania, Sclerocephalus, Loxomma, Rhinosaurus, Trematosaurus, Metopias, Capitosaurus, Mastodonsaurus, etc. Not only is there evident an increase of size of the squamosal but in some there occurs an overlapping of the supratemporal by the squamosal (*vide* Credner's figure of *Branchiosaurus amblystomum*, '81–'89, vol. 38, pl. 17, fig. 3).

I claim no novelty in transposing the prevailing use of the terms supratemporal and squamosal in the Stegocephala. Similar usage may be found in the papers of Baur, Ammon, Boulenger, and Broili. Baur ('86) compared the Stegocephalian skull with that of the Lacertilia as described by Parker and Bettany but afterwards returned to the

other nomenclature except that he used the term prosquamosal of Owen for the more external of the two elements. Ammon ('89) and Broili (:04) follow Baur's paper ('86) without advancing any arguments for this course. My contribution to the discussion is the advancement of new criteria for the determination of the squamosal bone.

I am well aware that this transposition of terms is likely to lead to confusion but it must be remembered that the confusion was introduced by others and that I am only returning to the proper terminology, for, as I think I have shown, the more lateral element is the homologue of the mammalian squamosal and must receive that name, while the element intervening between the squamosal and the parietal should according to the law of priority be called the supratemporal for Bakker ('22) first applied that term to the bone adjoining the parietal in the teleost skull and in the same sense it was used by Owen ('53) for the inner element of the temporal region of the Ichthyosaurs. Owen's ('65–'81) term prosquamosal which was adopted by Baur and other American students, is a synonym of squamosal and is consequently unnecessary.

The quadratojugal demands a moment's attention. In the Stegocephala this extends from the articular end of the quadrate to a greater or less distance dorsally upon its external surface, articulating anteriorly with the jugal (*J.*) and usually reaching also the maxillary (*Mx.*). Miall ('73, p. 236) states that in many Stegocephala (Mastodonsaurus, Archegosaurus, Trematosaurus, etc.) the quadratojugal forms the outer part of the articular surface for the lower jaw. In certain forms (*Sclerocephalus labyrinthicus, teste* Credner, '81–'89) this bone is separated from the quadrate by suture but in others according to Fraas ('89, pp. 54 and 72) quadrate and quadratojugal are indistinguishably fused. Broili (:04) thinks that the same is true for Eryops.

Another characteristic is that the quadratojugal is often overlapped from above by the squamosal, so that judging from the Stegocephala we may emphasize as its characters its close association with the articular end of the quadrate and its tendency to be covered by the squamosal. Is there any evidence of a bone with similar relations in the existing Amphibia?

Riese ('92) found that in *Tylotriton vermicosus* a bony process of the quadrate connects with the maxillary which is greatly lengthened

posteriorly and conjectured that this was a quadratojugal which had fused with the quadrate. Gaupp ('94, p. 102, footnote) writes: "Bei Triton wo ein Quadrato-jugale fehlt, beginnt trotzdem die Verknöcherung des Quadratum an der vorderen äusseren Ecke als perichondrale Knochenauflagerung — ein Verhalten das geeignet scheint, dem Quadrato-jugale noch eine besondere Bedeutung für die Verknöcherung des Quadratum zu zukennen." Kingsbury in 1903 and again in 1905 called attention to what seemed to be a separate ossification in Necturus, arising on the outer surface of the cartilaginous quadrate, and at first only partially covered by the squamosal. This ossification, which he first called the subsquamosal process of the quadrate, but later the "bone X," was at first distinct from the quadrate cartilage. Soon, however, it fused with the cartilage and from this place a zone of ossification extended around it, forming a ring of bone. In the larval Spelerpes practically the same conditions occurred except that in the adult this element was no longer distinguishable from the quadrate, all parts of which, with the exception of the articular surfaces, had ossified. From observations on Amphiuma, Amblystoma, and Desmognathus he concluded that this mode of ossification was at least frequent among the Urodeles.

FIG. D. — Transverse section through the otic region of Amphiuma, showing the quadratojugal ossification arising upon the external surface of the quadrate and covered to a large extent by the squamosal. *OC.*, otic capsule; *Qj.*, quadratojugal; *Qu.*, quadrate; *Sq.*, squamosal.

My observations on Necturus, Amblystoma, Triton, and Amphiuma confirm Kingsbury's account of the existence of this separate ossification. Figure D shows this bone (*Qj.*) as it occurs in Amphiuma. Now, since this bone is intimately associated with the quadrate, descending on its external surface nearly

to the articulation of the lower jaw, and is nearly covered by the squamosal, I would homologize it with the Stegocephalian quadratojugal.

Temporal Region of Reptilia.

In following out the modifications of the temporal region in the Reptilia I have endeavored to trace them according to the lines of descent, adopting for this purpose the ideas of Cope ('96) as modified

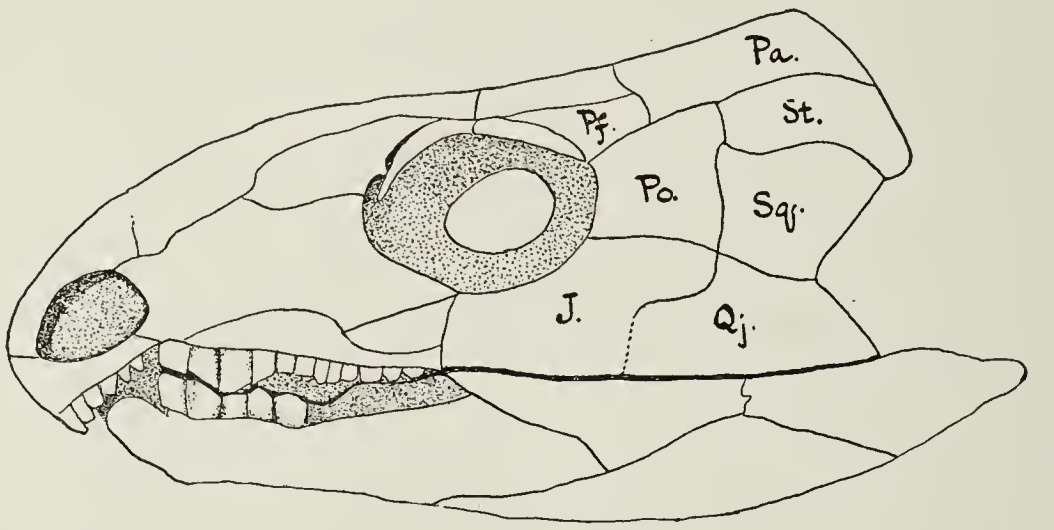

Fig. E. — Lateral view of the skull of *Pariotichus aguti*, after Cope, '95. *J.*, jugal; *Pa.*, parietal; *Pf.*, postfrontal; *Po.*, postorbital; *Qj.*, quadratojugal; *Sq.*, squamosal; *St.*, supratemporal.

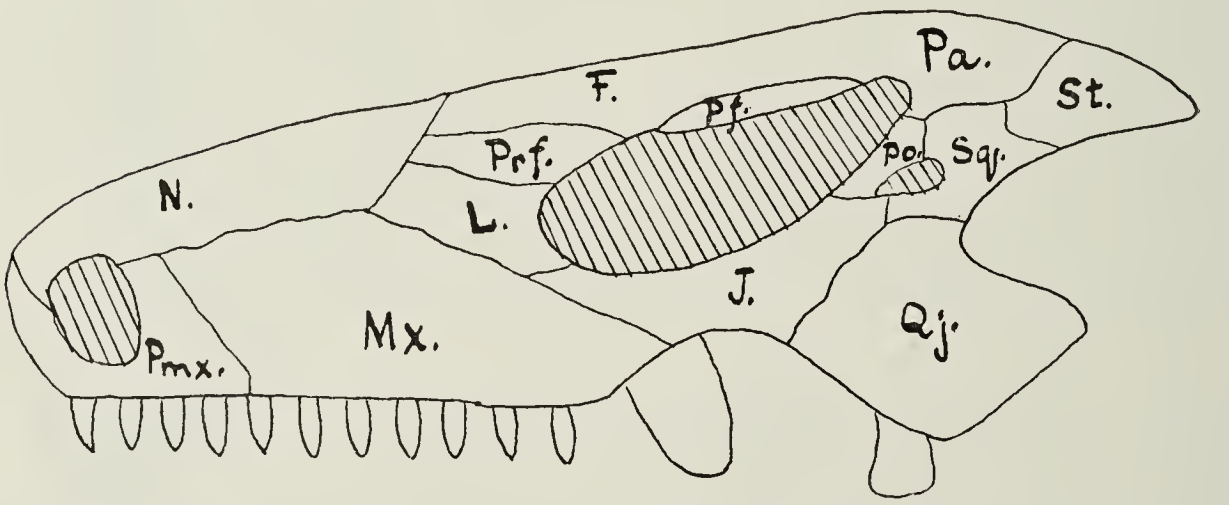

Fig. F. — Lateral view of the skull of Procolophon, from the restoration by Woodward. *F.*, frontal; *J.*, jugal; *L.*, lachrymal; *Mx.*, maxillary; *N.*, nasal; *Pa.*, parietal; *Pf.*, prefrontal; *Pmx.*, premaxillary; *Po.*, postorbital; *Prf.*, prefrontal; *Qj.*, quadratojugal; *Sq.*, squamosal; *St.*, supratemporal.

by Williston (: 04) except that I am not ready to trace the mammals through the Theriodontia.

Cotylosauria.— In the skull of the Cotylosauria (Cope, '80, p. 304, Pareiasauria; Seeley, '89) the most primitive of known reptiles there is practically the same arrangement of the elements in the temporal region as is found in the Stegocephala. There is here a complete bony roof consisting as there of supratemporal (fig. E, *St.*), squamosal (*Sq.*), and quadratojugal (*Qj.*), the homologies of these elements being complete. In Procolophon (fig. F), according to most authors, there is an exception to all other Cotylosauria in that there is a small vacuity in the bony roof between the postorbital (*Po.*), squamosal (*Sq.*), and jugal bones (*J.*) but in a letter quoted by Williston (: 04, p. 181) Broom apparently denies the existence of the gap. Yet it is in the proper place to be very suggestive of the infratemporal fossa of higher reptiles as has been mentioned by several authors (Seeley, '89; Woodward, '98, p. 148, and others).

Ichthyosauria.— The Ichthyosaurs, so far as is indicated by the

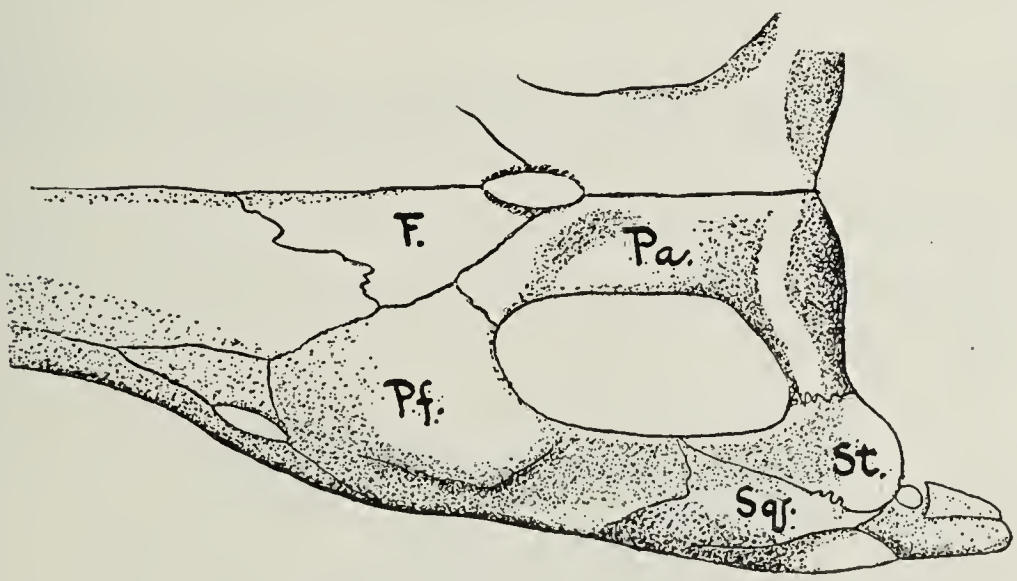

FIG. G. — Dorsal view of the left posterior part of the skull in *Ichthyosaurus acutirostris*, from Zittel after Owen. *F.*, frontal; *Pa.*, parietal; *Pf.*, prefrontal; *Sq.*, squamosal; *St.*, supratemporal.

temporal region, stand closest of all reptiles to the Cotylosauria. The supratemporal (figs. G, H, I, *St.*) is separated anteriorly from the parietal by a vacuity, the supratemporal fossa, but there cannot be any doubt as to the homologies of supratemporal, squamosal (*Sq.*), and quadratojugal (*Qj.*) since, in other respects, these have the same relations as in the Cotylosaurs. The supratemporal (squamosal, Auctorum) joins anteriorly the postfrontal (*Pf.*), laterally the squamosal, and posteriorly is produced medially to reach the parietal. The squamosal articulates anteriorly with the postorbital, laterally

with the quadratojugal and covers the dorsal external surface of the quadrate (figs. H and I). Lateral and ventral to the squamosal and lying upon the lower external surface of the quadrate is the quadrato-

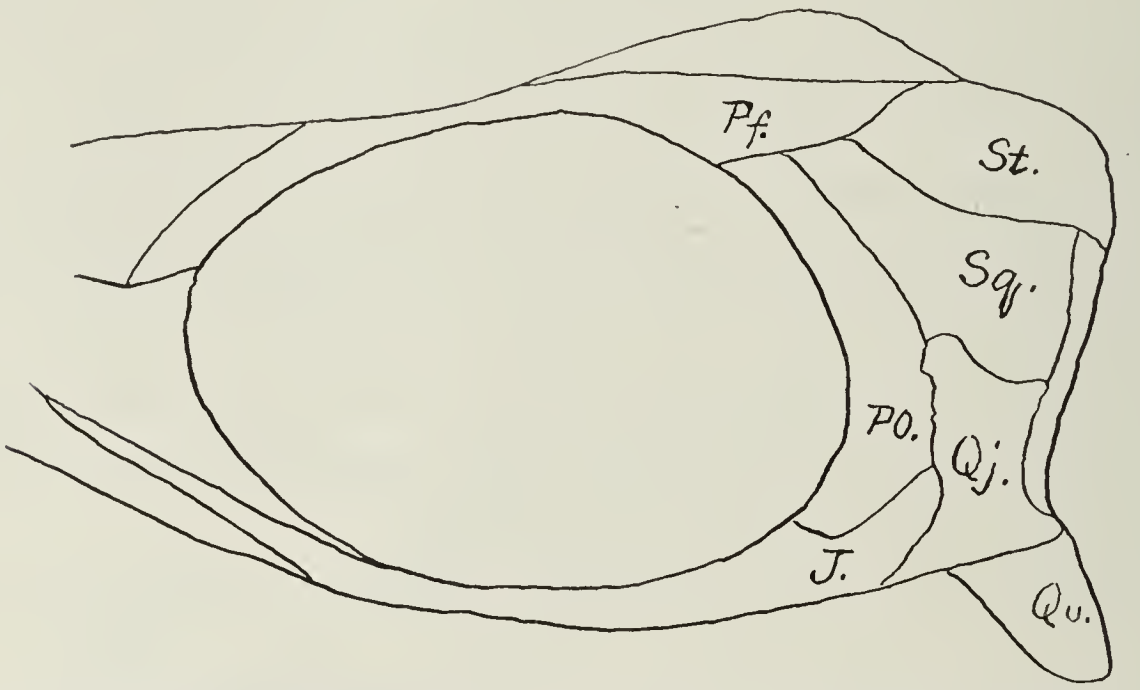

Fig. H. — Posterior lateral aspect of the skull of *Ichthyosaurus longifrons*, from Williston after Owen. *J.*, jugal; *Pf.*, postfrontal; *Po.*, postorbital; *Qj.*, quadratojugal; *Qu.*, quadrate; *Sq.*, squamosal; *St.*, supratemporal.

jugal which joins in front both the jugal and the elongate postorbital. The supratemporal fossa lies between supratemporal, parietal, and postfrontal.

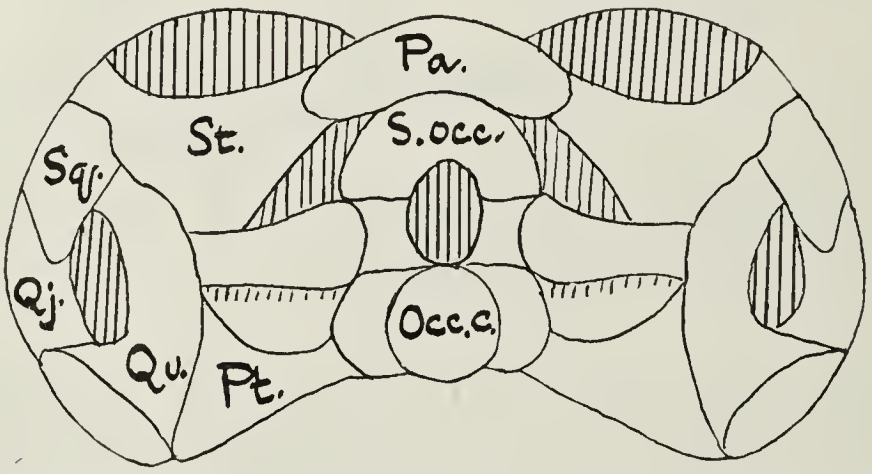

Fig. I. — Skull of *Ichthyosaurus longifrons* from the posterior aspect, after the restoration by Woodward. *Occ. c.*, occipital condyle; *Pa.*, parietal; *Pt.*, pterygoid; *Qj.*, quadratojugal; *Qu.*, quadrate; *S. occ.*, supra-occipital; *Sq.*, squamosal; *St.*, supratemporal.

Testudinata.— Although no Testudinata are known earlier than the Jurassic, the order seems to be a very old one and to represent a side branch from the primitive reptilian stock, a view which receives

confirmation from the observations of Case (: 05). In some (Amphichelydia, Cheloniidae, Dermochelydidae) there is a complete bony roof in the temporal region resembling considerably that found in the Cotylosaurs, except that instead of three, only two elements occur. Baur ('89), reasoning from this condition, attempted to explain the structures existing in other Testudinata by supposing that supra- and infratemporal fossae were never developed in the order, but that the original bony roof suffered diminution by absorption from behind, between squamosal and parietal (*e. g.*, Chelydridae, Dermatemydidae, Staurotypidae, Cinosternidae, Platysternidae, Emydidae, Testudinidae, Trionychia). But, simultaneously with this absorption, a reduction or loss occurred from below between quadrate and jugal, resulting in the formation of a slender arch which in a few cases (Terrapene, Geoemyda) was entirely reduced. In other cases reduction took place entirely from below leaving the squamosal and parietal either in contact as in the Chelydidae, or destroying the connection as in Chelodina.

Plausible as this may be, it is by no means proven, and to-day there is great uncertainty as to the homologies of the two bones of the Testudinate temporal region. The more ventral element called by Hallmann the quadratojugal (temporal écailleux of Cuvier; squamosal, Owen, '66–'68) and so regarded by the majority of authors, has been called the paraquadrate by Gaupp ('94) and thus homologized with the bone in the Stegocephala and Cotylosauria which lies dorsal and medial to the true quadratojugal, a view which has been followed by Siebenrock (*teste* Rabl), Wiedersheim (: 06), etc. The more medial element (mastoïdien, mastoid, of Cuvier and Owen) is usually termed the squamosal and thus homologized with that bone which in the Cotylosaurs I have shown to be the supratemporal. Baur ('89, p. 472) using the nomenclature of the present paper, held that the turtles lack a supratemporal bone while Williston (: 04) thinks that the squamosal (his prosquamosal) is absent, its function being taken by the quadratojugal.

The questions involved can only be settled by study of the development of the bones of this region or by the discovery of more primitive types of Testudinata.

Rhynchocephalia.— Before considering the skull of Sphenodon it is best to consider some of the more primitive members of this order, where, although exact knowledge of the temporal region is not abun-

dant, enough is known to aid us in understanding conditions in the existing genus.

Sauranodon incisivus (fig. J) from the Jurassic beds of the Rhone is apparently the most primitive type known since it lacks both supra- and infratemporal fossae, but Lortet's ('92) accounts and figures are not easy to follow, and in some points are not easily reconciled with each other. Lortet's description of the parts in question runs: "En arrière [les pariétaux] soudent, sur la ligne médiane avec les occipitaux supérieurs, tandis qu'en dehors, ils envoient en arrière, et en

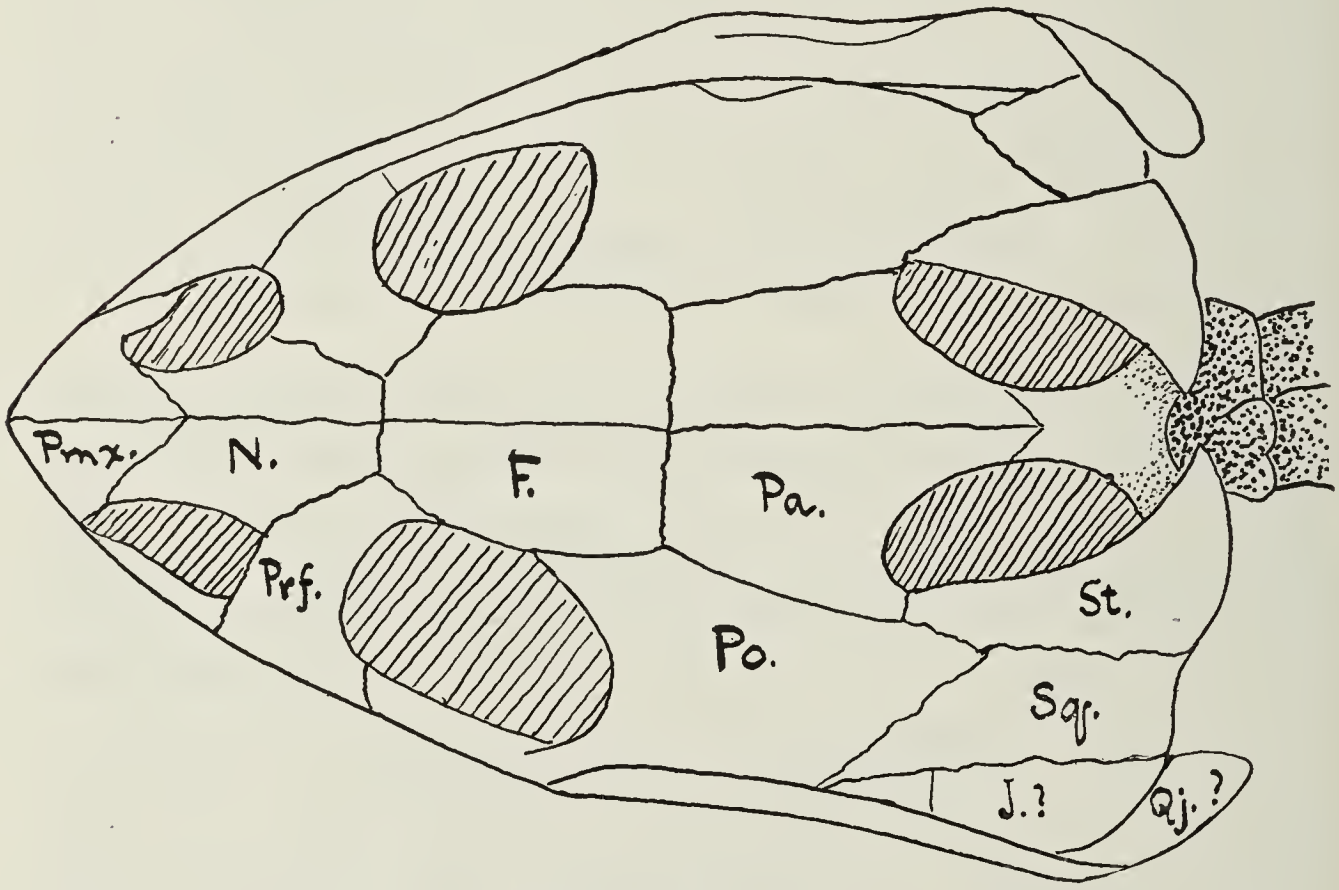

FIG. J. — Dorsal view of the skull of Sauranodon, after Lortet. *F.*, frontal; *J?*, jugal?; *N.*, nasal; *Pa.*, parietal; *Pmx.*, premaxillary; *Po.*, postorbital; *Prf.*, prefrontal; *Qj?*, quadratojugal?; *Sq.*, squamosal; *St.*, supratemporal.

dedans une longue apophyse concourant à la formation des parties latérales et externes de la fosse occipitale. Ces apophyses, longues de 12 millimètres, ont une largeur maxima de 10 millimètres. En arrière, ces apophyses très remarquables se rejoignent presque sur la ligne médiane en formant de véritables crochets qui viennent presque se toucher au-dessus de l'occipital supérieur, long lui-même de 4 millimètres et manifestement bifide dans sa partie postérieure." But Boulenger ('93) has pointed out (and a study of the figure seems to justify him) that Lortet's "apophyses de pariétaux" are really the supratemporals.

Lortet's 'apophyse' (*St.*) forms the external boundary of the post-temporal fossa and articulates anteriorly with the parietal (*Pa.*), (but from Lortet's figure is clearly distinct from it) and externally with the postorbital (or postfrontal, *Po.*) and with the posteriorly placed squamosal (*Sq.*, temporal of Lortet). In its posterior extension it bends medially over the supra-occipital (posterior processes of the parietal of Baur, '94) nearly reaching its fellow of the opposite side (a condition possibly due to dislocation of parts). It can have no relation to the external surface of the quadrate, neither does it articulate with the postorbital (*Po.*) in a manner characteristic of the squamosal in the Stegocephala and Cotylosauria, but it agrees with the supratemporal in position and relations and, as Boulenger has suggested, should be called by that name.

Lateral to the supratemporal (fig. J, *St.*) is a second bone (*Sq.*), the temporal of Lortet, prosquamosal of Baur ('94) and Osborn (:03) which, according to Lortet, articulates with the quadrate ("s'articulant en arrière avec un os carré") but it is not certain what he regards as the quadrate, and there is nothing in his figure which I can interpret as such. In front, it articulates with the postorbital while

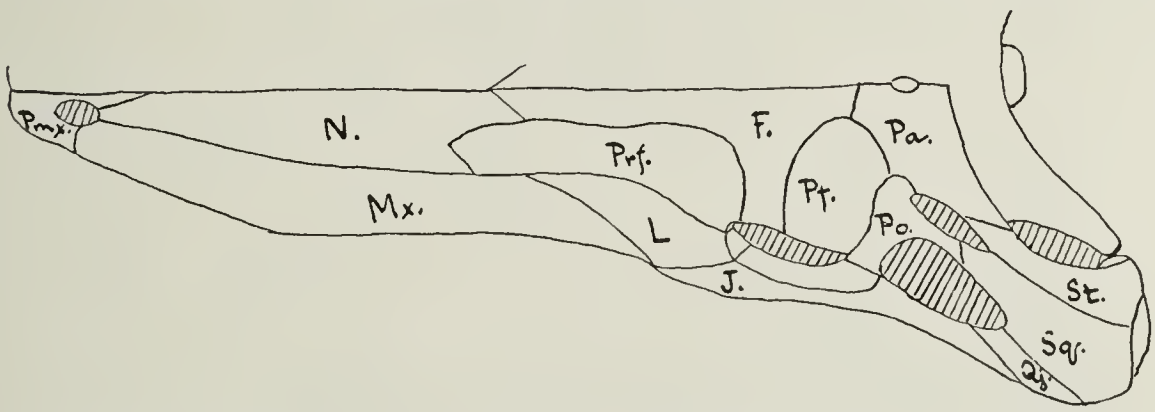

FIG. K. — Restoration of the skull of the Pelycosauria, from above, after Baur and Case. *F.*, frontal; *J.*, jugal; *L.*, lachrymal; *Mx.*, maxillary; *N.*, nasal; *Pa.*, parietal; *Pf.*, postfrontal; *Pmx.*, premaxillary; *Po.*, postorbital; *Prf.*, prefrontal; *Qj.*, quadratojugal; *Sq.*, squamosal; *St.*, supratemporal.

the parts with which it is connected laterally are not so easy to determine. Comparison with the Stegocephalian skull (*e. g.*, Branchiosaurus, fig. C) would seem to indicate that the element lateral to the left temporal is the jugal (*J.*) while on the posterior lateral margin of this is the quadratojugal. These facts, and especially the relation to the quadrate, if Lortet's account be accepted, demonstrate this element to be the squamosal.

In the Pelycosauria (figs. K and L) there occurs not only a post-

temporal but supra- and infratemporal fossae as well, while squamosal, supratemporal, and quadratojugal bones persist, thus indicating a position intermediate, so far as the temporal region is concerned, between Sauranodon on the one hand, and Palaeohatteria, Stenometopon, and Sphenodon on the other, in which, while the three fossae occur, the supratemporal bone has disappeared.

In Dimetrodon (fig. L) as reconstructed by Case ('98) the supratemporal (squamosal of Case and of Williston) articulates laterally with the squamosal (prosquamosal of Case, quadratojugal of Williston) and, by joining the short posterior process of the parietal, forms the

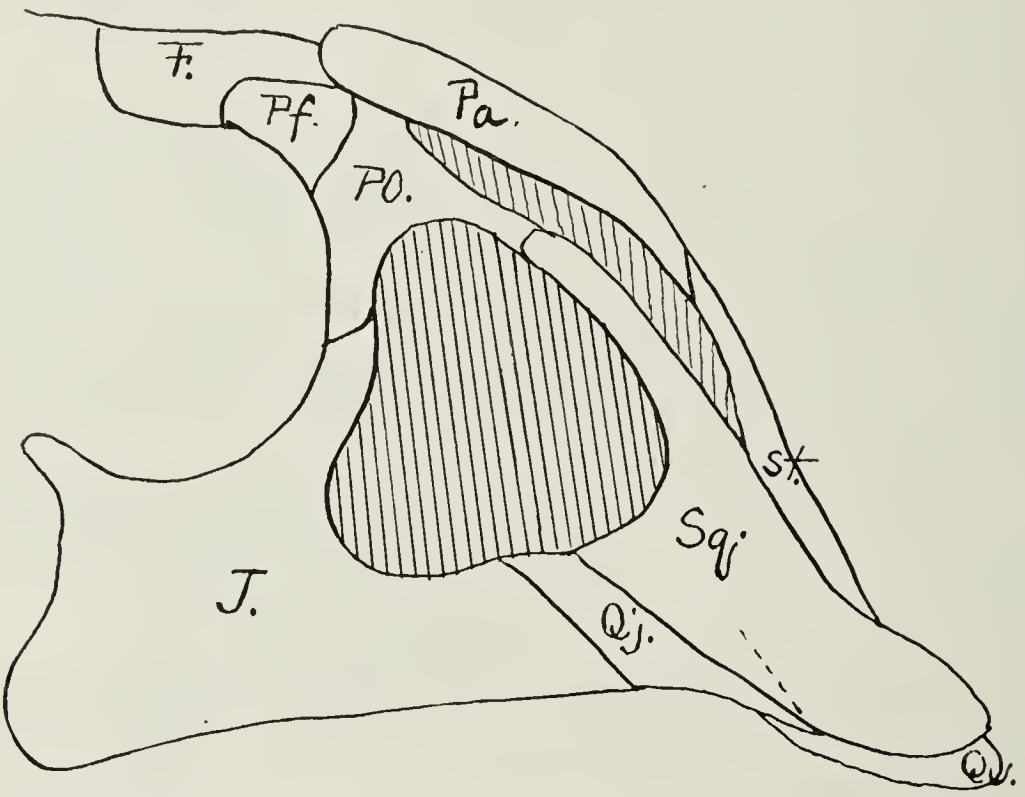

FIG. L. — Posterior lateral view of the skull of Dimetrodon, after the reconstruction of Case. *F.*, frontal; *J.*, jugal; *Pa.*, parietal; *Pf.*, postfrontal; *Po.*, postorbital; *Qj.*, quadratojugal; *Qu.*, quadrate; *Sq.*, squamosal; *St.*, supratemporal.

lateral border of the post-temporal and the postero-median border of the supratemporal fossa. Lateral to the supratemporal and overlying the quadrate (*Qu.*) is the squamosal (*Sq.*) bounded on its ventrolateral margin by the quadratojugal. It articulates, also, with the postorbital (*Po.*) forming with the later the arcade separating supra- and infratemporal fossae. The quadratojugal (prosquamosal of Williston) is intercalated between jugal, squamosal, and quadrate.

The relations in Palaeohatteria, Stenometopon, and Sphenodon are so nearly alike that they may be conveniently considered together.

The skull of Sphenodon (fig. M) has been studied by Günther, Baur, Siebenrock, Osawa, Schauinsland, Howes and Swinnerton, and others.

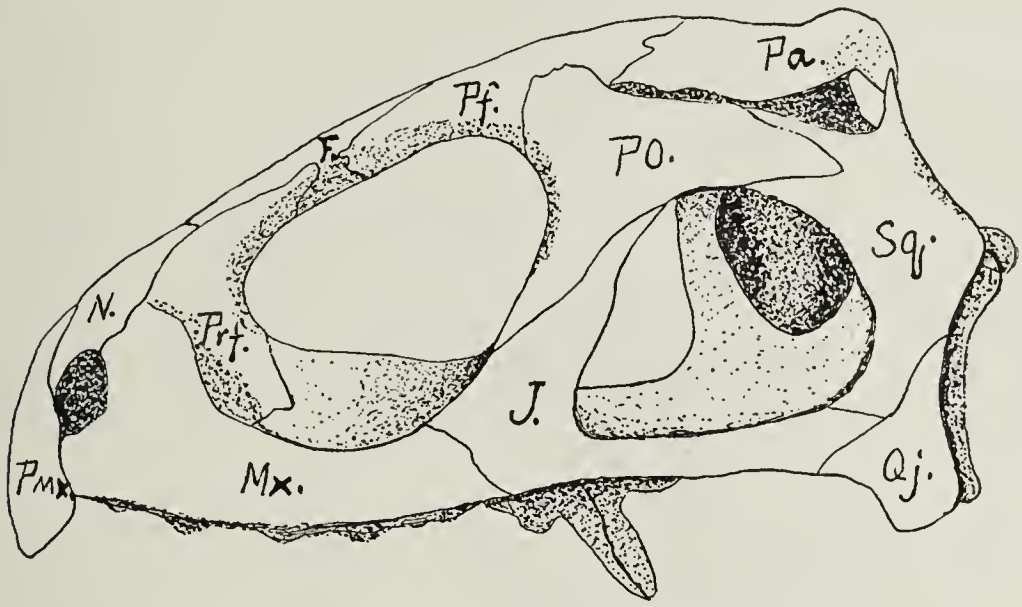

FIG. M. — Lateral view of the skull of *Hatteria punctata*, after Rabl. *F.*, frontal; *J.*, jugal; *Mx.*, maxillary; *N.*, nasal; *Pa.*, parietal; *Pf.*, postfrontal; *Pmx.*, premaxillary; *Po.*, postorbital; *Prf.*, prefrontal; *Qj.*, quadratojugal; *Sq.*, squamosal.

Both supra- and infratemporal fossae exist hence there are two bony arcades. The upper arcade separating the two fossae is composed of the postorbital (*Po.*) and an element (*Sq.*) which according to Howes and Swinnerton (:01) and Schauinsland (:00) develops on the lateral surface of the otic capsule (fig. N) and later extends down upon the dorsal external surface of the quadrate (fig. O). From the fact that this bone shows intimate relations with both otic capsule and quadrate, that it connects anteriorly with the jugal (*J.*) and the postorbital (*Po.*) to form the ventral and dorsal arcades it cannot be regarded as other than the squamosal, its late association with the quadrate being the only deviation from what we have seen to be squamosal characteristics. The same relations hold for the bone in Palaeohatteria and Stenometopon usually

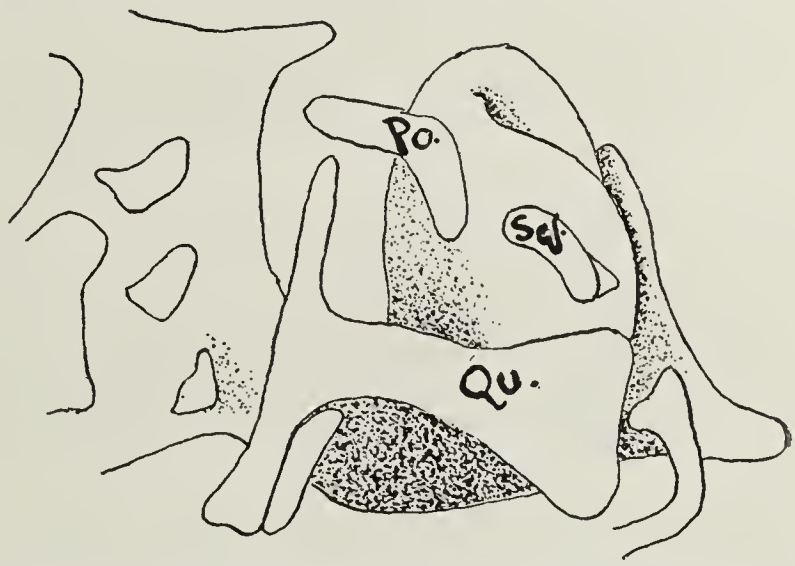

FIG. N. — Lateral view of the developing skull of Sphenodon (Hatteria), after Howes and Swinnerton. *Po.*, postorbital; *Qu.*, quadrate; *Sq.*, squamosal.

called the squamosal. In Sphenodon, by the time the adult condition is reached the squamosal has extended a dorsal process to the parietal (fig. P) thus resembling to a certain extent the condition found in Amphiuma (pl. 40, fig. 4) so that this element in its relations exhibits characters of both squamosal and supratemporal, relations which led Baur to maintain that both elements were present in the single bone. The development, however, shows that this supposition is untenable (*vide* Howes and Swinnerton, :01).

The reconstruction of Palaeohatteria by Woodward ('98, p. 185) shows no such process to the squamosal but the sides of the parietal (represented by Credner, '81–'89, by dotted lines) are produced to meet

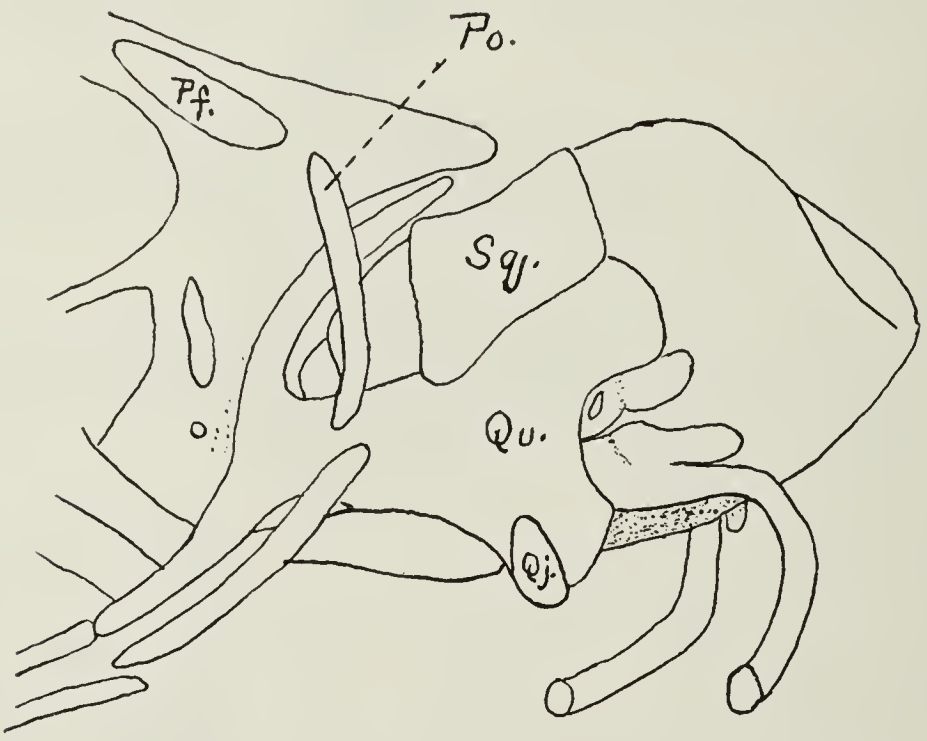

FIG. O. — Lateral aspect of developing skull of Sphenodon (Hatteria), but a somewhat older stage than that represented in Fig. N, after Schauinsland. *Pf.*, postfrontal; *Po.*, postorbital; *Qj.*, quadratojugal; *Qu.*, quadrate; *Sq.*, squamosal.

the squamosal. Apparently the same is true for Stenometopon. The differences between the living and the fossil genera are that in Sphenodon with the loss of the supratemporal, the squamosal has been produced to meet the parietal while in the other genera mentioned, an outgrowth from the parietal extends to the squamosal.

The squamosal in Sphenodon is the mastoid of Günther, the supratemporal of Siebenrock ('93), the paraquadrate of Gaupp, and the squamosal of most other authors.

The lower arcade in Sphenodon is formed of jugal and squamosal,

while a third element, usually called the quadratojugal occurs lateral and ventral to this junction. It covers the external surface of the articular end of the quadrate, but Osawa ('96, pp. 449 and 520) calls it the tympanic.

Comparisons of the skulls of Sauranodon, the Pelycosauria, Palaeohatteria, Stenometopon, and Sphenodon can lead only to the conclu-

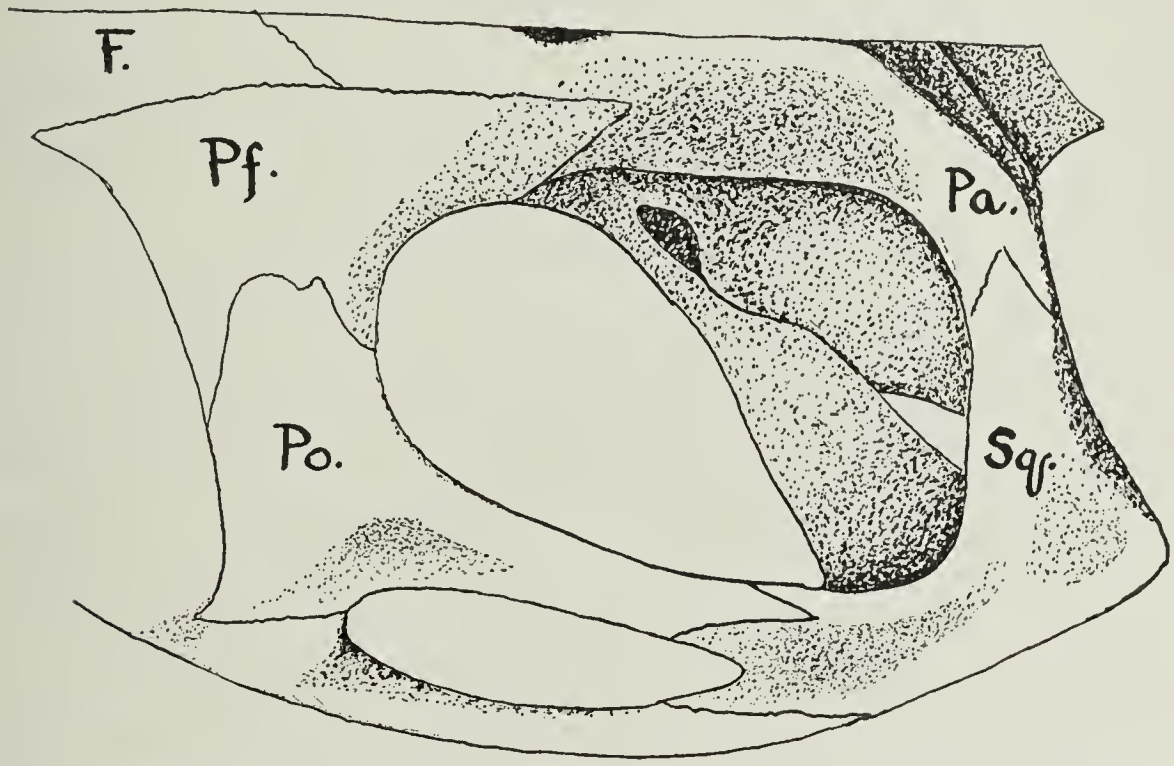

FIG. P. — The posterior dorsal aspect of the left side of the skull in Sphenodon (Hatteria), after Rabl. *F.*, frontal; *Pa.*, parietal; *Pf.*, postfrontal; *Po.*, postorbital; *Sq.*, squamosal.

sion that in the phylogenetic development of the last genus it is the medial (supratemporal) rather than the lateral (squamosal) of the two problematic elements that has been lost. The lateral in Sauranodon articulates with jugal, quadratojugal, postorbital, and quadrate, the medial with only the parietal and postorbital. The progressive enlargement of the supratemporal fossa must result in a corresponding decrease and final loss of the supratemporal, while the necessity of retaining strength in the cranial roof would cause a corresponding development of processes from either parietal or squamosal to meet the other element. The view that the lower or squamosal has disappeared involves numerous difficulties. While retaining its connection with the parietal, the supratemporal must at the same time gain connections with jugal, quadratojugal, postorbital, and quadrate almost exactly duplicating those of the last element, a case of substitution rather difficult to imagine.

It may be noted that Williston has apparently fallen into error when he says (: 04, p. 188) that in Sphenodon "the prosquamosal has utterly disappeared even in the embryo, according to Howes and Swinnerton." These authors call the prosquamosal of Williston the squamosal, his squamosal the supratemporal, and they nowhere say that it is the lateral of these two elements (Williston's prosquamosal) which has disappeared but incline strongly to the view that it is the other element which has been lost.

Squamata.— The Squamata, including the suborders Lacertilia, Dolichosauria, Pythonomorpha, and Ophidia, are generally supposed to have been derived from a Rhynchocephalian ancestor.

The temporal region of the skull in the Lacertilia has been frequently studied and very different views of the homologies of the elements have been advanced. I have studied the development of the bones in the skull of Sceloporus and find that in their relations they agree fairly well with the account given by Gaupp ('94) for *Lacerta agilis*, although we differ greatly in our interpretations. In figure 5 (pl. 41) is represented the temporal region of an embryo of Sceloporus in which the centers of ossification have just appeared. Lateral and ventral to the parietal (*Pa.*) are two bones. The more dorsal (*St.*) develops as a mere rod upon the otic capsule above the dorsal margin of the quadrate (*Qu.*) and extends from the parotic process of the exoccipital forward to the posterior process of the parietal with which it is closely associated from its first appearance. Further, it lies dorsal to an element which I shall soon show to be the squamosal. Hence in all its relations it is clearly the supratemporal. It has been called the mastoid (Cuvier, Stannius, '46, Owen), squama temporalis (Hallmann, Stannius, '56), squamosal (Gegenbaur, Baur, '91 and '94, Wiedersheim, '93, Gaupp, Gadow, Williston, and others), the opisthotic (Cope, '71), the paroccipital (Cope, '72), and the supratemporal (Parker and Bettany, Baur, Hoffmann, Siebenrock, and Woodward).

The lower or more lateral element has been called the temporal écailleux (Cuvier), quadratojugal (Hallmann, Stannius, Holland, Gegenbaur, Wiedersheim, Baur, '89, and others), the supratemporal (Cope, '92, and Gadow), squamosal (Owen, Huxley, Parker and Bettany, Cope, '71, Baur, '87, Siebenrock, and Woodward), the paraquadrate (Gaupp), and the prosquamosal (Baur, '94, and Williston). In the stage of figure 5 (pl. 41) it consists of an anterior portion, which articulates with the postorbital (*Po.*) and is thus indirectly

connected with the jugal (not shown in the figure), and of a posterior portion which develops upon the otic capsule and with its posterior end overlaps the anterior dorsal portion of the quadrate (*Qu.*). It thus fully meets the definition of the squamosal as given on the foregoing page.

In the adult of the same genus (pl. 41, fig. 6) the anterior half of the supratemporal (*St.*) is closely applied to the distal external surface of the posterior process of the parietal (*Pa.*). Its posterior inner surface adjoins the exoccipital, while a large part of its external surface is hidden from view by the hinder portion of the squamosal (*Sq.*) which lies across it. The squamosal in turn extends forward under the ventral margin of the postorbital (*Po.*) and nearly meets the posterior end of the jugal (*J.*). If now we compare these relations with the conditions given by Baur and Case ('99) in their restoration of the Pelycosaur skull (fig. K) we find that in general they are easily reconciled with each other. In both, the supratemporal vacuity is bounded anteriorly by the postorbital (*Po.*), ventrally by the postorbital and squamosal (*Sq.*), behind by the supratemporal (*St.*), and dorsally by the supratemporal and parietal (*Pa.*). In Sceloporus, however, the supratemporal has undergone marked reduction and this seems to be true of the Lacertilia as a whole, while in Sphenodon it has disappeared entirely. If we accept Williston's (:04) homologies, the posterior and ventral boundary of the supratemporal fossa in the Lacertilia cannot be homologous with that in the Rhynchocephalia, while accepting the interpretations of the present article they are compared without difficulty. The ventral boundary of the infratemporal fossa of the Rhynchocephalia is lost in the modern lizard.

The figures of Platycarpus and Liodon as given by Zittel (:02, vol. 2, p. 158; '87–'90, vol. 3, p. 615) show that in the Pythonomorphs we have practically the same conditions and relations as in the Lacertilia.

In the skull of the adult Ophidia there is but a single covering bone in the temporal region lateral to the parietal and for this as many homologies have been given as for either of the two in the lizards. It is the mastoid of Cuvier and Owen. Hallmann, Stannius ('56), Huxley, Gaupp, Gegenbaur, Gadow, Williston, and many others have called it the squamosal; Boulenger has termed it the supratemporal and Cope the paroccipital. It develops upon the otic capsule and is in close proximity anteriorly with the parietal, even in the embryo. It shows no signs of overlapping the quadrate but rather

extends slightly medial to it. The similar relations of this and the medial element in the lizard are at once evident and show that it must be regarded as the supratemporal.

In this connection it is worthy of note that Parker ('78, p. 406) says that in ripe embryos of Tropidonotus "inside the middle of the squamosal there is a small suboval scale of bone, the supratemporal, here it is only distinct for a time, but in the lizard permanently so." Parker gives no reference to figures and so it is difficult to say exactly what he means, especially since he ('79) has become confused in the terminology of the temporal elements in the lizard. He ('78, pl. 31, fig. 7), however, gives a figure in which an oval scale is shown ventral to the 'squamosal' (my supratemporal), and this, it may be, is the true

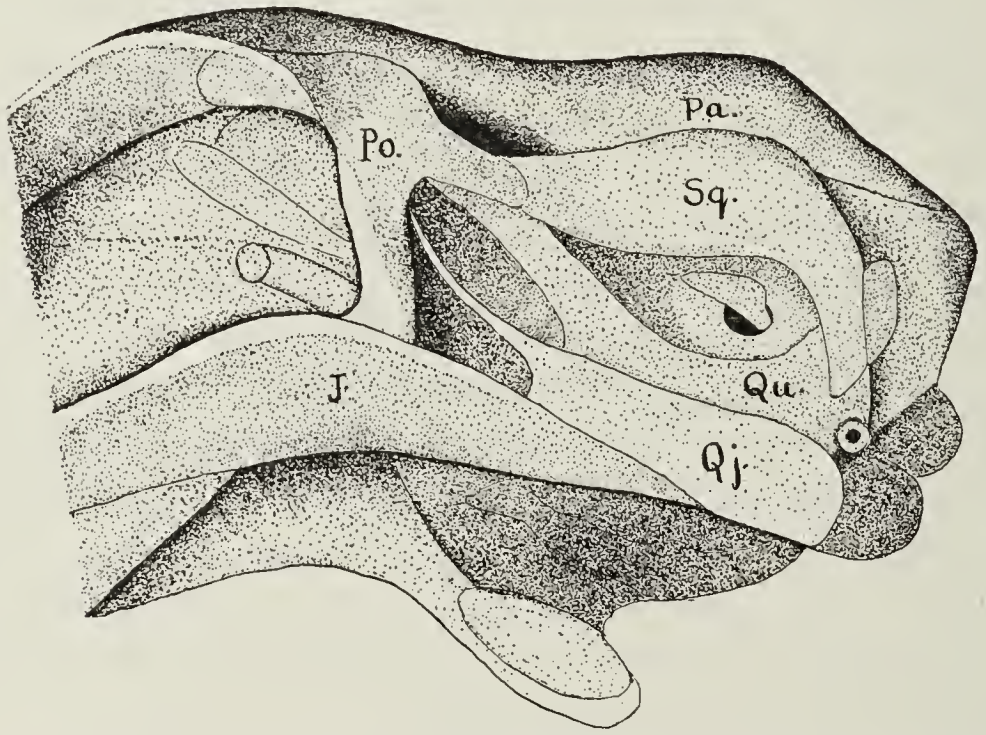

FIG. Q. — Side view of the skull of *Crocodilus palustris* (embryo 10 inches long), after Parker. *J.*, jugal; *Pa.*, parietal; *Po.*, postorbital; *Qj.*, quadratojugal; *Qu.*, quadrate; *Sq.*, squamosal.

squamosal, since, by comparison with the lizard, it lies in the proper position for that bone. If this be true then there can be no doubt that the bone which persists in the adult is the supratemporal. It should not be forgotten that Gaupp ('94, p. 87, footnote) was not able to find this bone in the one stage of Tropidonotus at his command.

Crocodilia.— In the temporal region of the Crocodilia there are, as a rule, two arcades and two temporal vacuities. The upper arcade (fig. Q) is formed by the postorbital (*Po.*) and a bone (*Sq.*) occupying the postero-lateral superior angle of the skull. Cuvier called this the

mastoid and in this he was followed by Stannius ('46), Owen ('66–'68), and others. Hallmann, however, homologized it with the mammalian squamosal (squama temporalis) and since his day it has been generally known as the squamosal.

According to Parker, whose figures I have reproduced, this element develops in *Crocodilus palustris* (fig. Q) upon the otic capsule, and here, as in the alligator (fig. R) extends down upon the dorsal external surface (otic process) of the quadrate. Parker gives no evidence, in either text or figures, as to whether this is the condition in the young

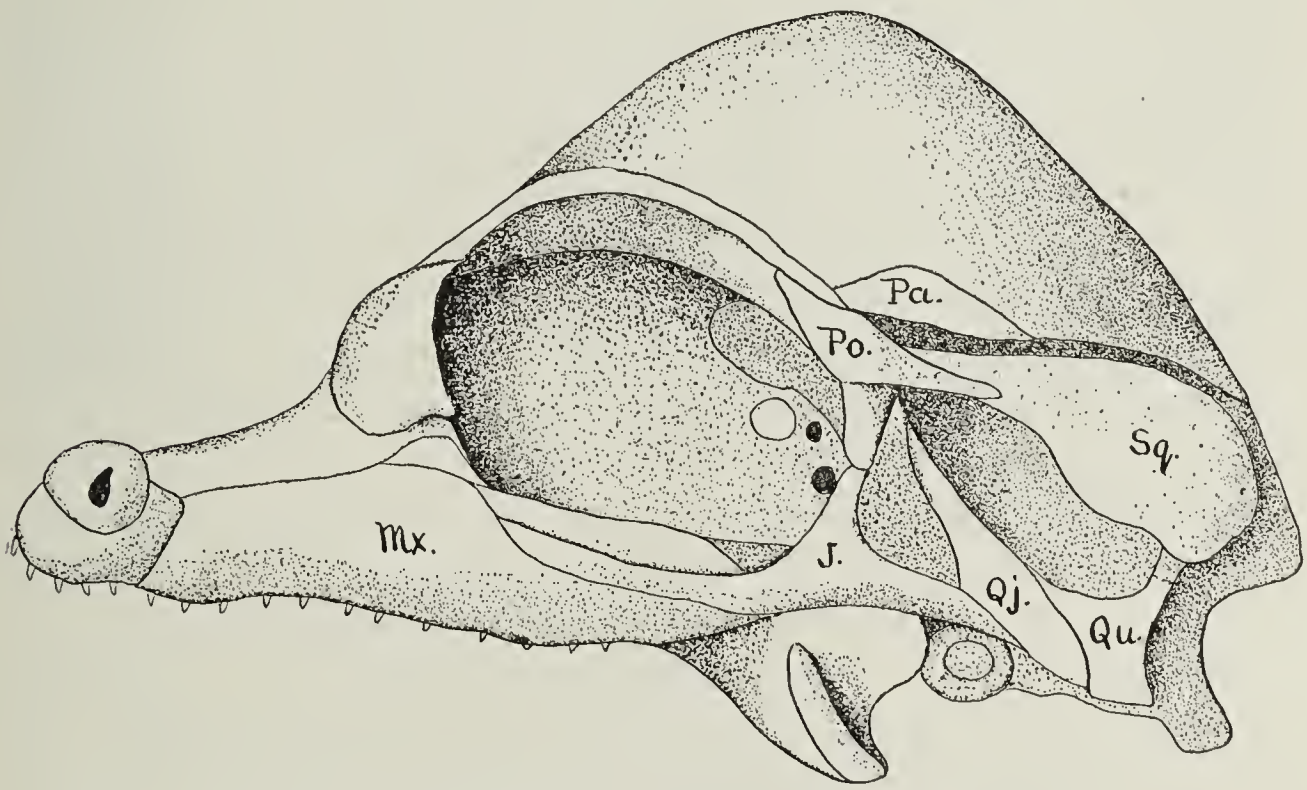

FIG. R. — Side view of the skull of *Alligator mississippensis* (large embryo), after Parker. *J.*, jugal; *Mx.*, maxillary; *Pa.*, parietal; *Po.*, postorbital; *Qj.*, quadratojugal; *Qu.*, quadrate; *Sq.*, squamosal.

or whether it is reached in the later stages alone. If the latter, it only parallels the condition in Sphenodon. From these early facts as well as its position lateral to the supratemporal fossa and its articulation with the postorbital, I can but agree with the majority in regarding it as the squamosal.

The lower arcade is formed of two bones, an anterior jugal (*J.*) which articulates in front with the maxillary and is produced behind to meet the second element (*Qj.*), which was called the temporal écailleux by Cuvier, the quadratojugal by Hallmann, the squamosal by Owen ('66–'68), and the paraquadrate by Gaupp. Gaupp came to this conclusion by a comparison with Sphenodon when he regarded

it as homologous with the part which I regard as the squamosal in that genus. But if I have correctly identified the squamosal in the Crocodilia, the element is in the right position for the quadratojugal, an interpretation which is supported by its covering the lower external surface of the quadrate adjacent to the articular surface. A comparison of this bone in the Crocodilia (figs. Q and R) with the quadratojugal in Dimetrodon shows at once almost identical relations except that in the Crocodilia the quadratojugal has been produced upwards and forwards across the infratemporal fossa, actually joining the postorbital by a special process. Gaupp ('94) reasoning from the relationships of this bone (quadratojugal) in Gavialis, where it joins the postorbital directly below the squamosal, considered that this showed a primitive condition of the element (his paraquadrate) which lies above the quadratojugal in the lower forms and thus prevented him from considering it as the quadratojugal. To me, however, it is far more plausible so to consider it and to regard the process which joins it in Alligator and Gavialis to the postorbital as secondary in character and correlated with the extension inwards and forwards of the quadrate.

The supratemporal has disappeared in the skull of the Crocodilia.

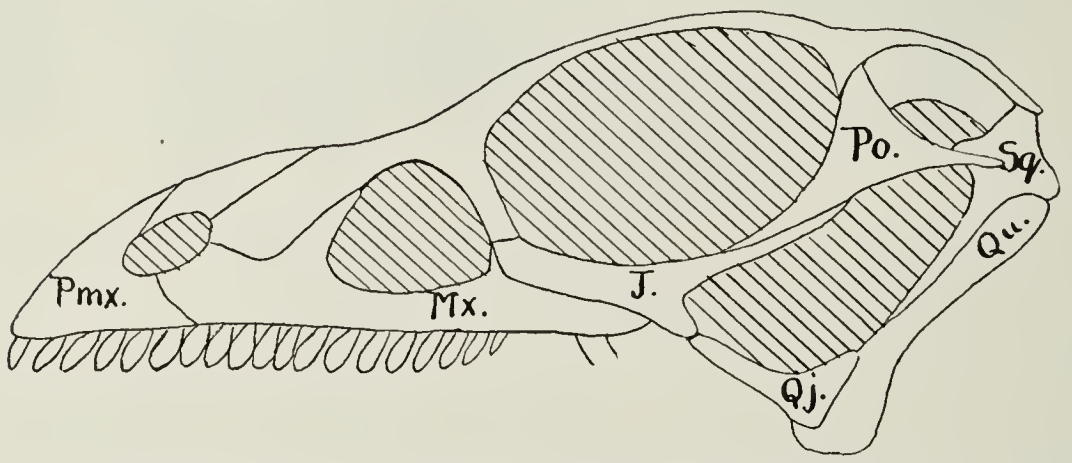

FIG. S. — Lateral aspect of the skull of Anchisaurus, after Marsh. *J.*, jugal; *Mx.*, maxillary; *Pmx.*, premaxillary; *Po.*, postorbital; *Qj.*, quadratojugal; *Qu.*, quadrate; *Sq.*, squamosal.

Baur ('94), however, maintained that the squamosal was a complex of the 'squamosal' (supratemporal) and 'prosquamosal' (squamosal proper), but as in the case of his similar supposition with regard to Sphenodon, no embryological evidence has yet been advanced for the existence of the second bone.

Dinosauria.— Two arcades are found in the temporal region of the Dinosaur skull (fig. S) and these are generally regarded as homol-

ogous with those of the Rhynchocephalia and Crocodilia. Further, almost all authors are agreed in saying that of the three temporal elements (supratemporal, squamosal, quadratojugal) of the primitive reptiles (Cotylosauria) the middle one has disappeared, only the medial and the lateral ones persisting.

In this I believe them to be in error. If it be the supratemporal that has disappeared in the Rhynchocephalia and Crocodilia, as I have attempted to prove, we should hardly expect it to reappear in the Dinosaurs, an order which is usually regarded as having had these for its ancestors. In many of the Dinosaurs the upper of the two temporal bones extends beyond the otic capsule sufficiently to cover the head of the quadrate. In others (Anchisaurus, fig. S) it extends for some distance down beside the quadrate and in a few (Ceratosaurus, Baur, '91, p. 446; Ceratops, Marsh, '96, p. 210) we find that it actually enlarges so as to articulate with the quadratojugal.

From this evidence of its relation to the otic capsule, quadrate, quadratojugal, and its articulation with the postorbital, and the ancestral history of the group, I prefer, until more proof to the contrary is advanced, to regard the upper of the two elements as the squamosal.

Theriodontia, Anomodontia, and Sauropterygia.— It now remains to return to the Cotylosauria and to follow out that line of reptiles, the so called Theromorpha, which many claim has given rise to the Mammalia, but which will be considered here as a side branch that early became extinct. Besides the so called mammalian characteristics (to be explained by parallel development), the Theriodontia are generally recognized as intermediate between the Cotylosauria on the one hand and the Anomodontia and Sauropterygia on the other.

The investing bones of the temporal region of the Theriodonts (fig. T) form a broad arcade which bounds the supratemporal vacuity externally and below. This arcade is composed of a jugal (*J.*) and a second bone (*Sq.*), almost universally regarded as the squamosal. It covers the external surface of the quadrate nearly or quite to its articular end, extends upon the otic capsule, and connects with the parietal by a narrow process.

In the temporal region of the Anomodontia and the Sauropterygia we find practically the same condition as in the Theriodontia. A large bone covers the external surface of the quadrate, even entering into articulation with the articular, and extending dorsally to join the parietal. In front, it articulates with either the postorbital or the

jugal, or with both to form a broad arcade which bounds the large supratemporal vacuity below.

From the relations of this bone in these three orders to quadrate, otic capsule, and the postorbital (or the jugal by a recession of the postorbital) it must be regarded as the squamosal. Hence it follows that the upper or more medial element, the supratemporal of the Cotylosaurs (as well as the quadratojugal) is unrepresented unless fused with the squamosal. In Cynognathus (fig. T) there is in the published figures an infratemporal fossa (its existence is denied by Broom) and the position of this when compared with Procolophon further strengthens the conclusion that it is the true squamosal which

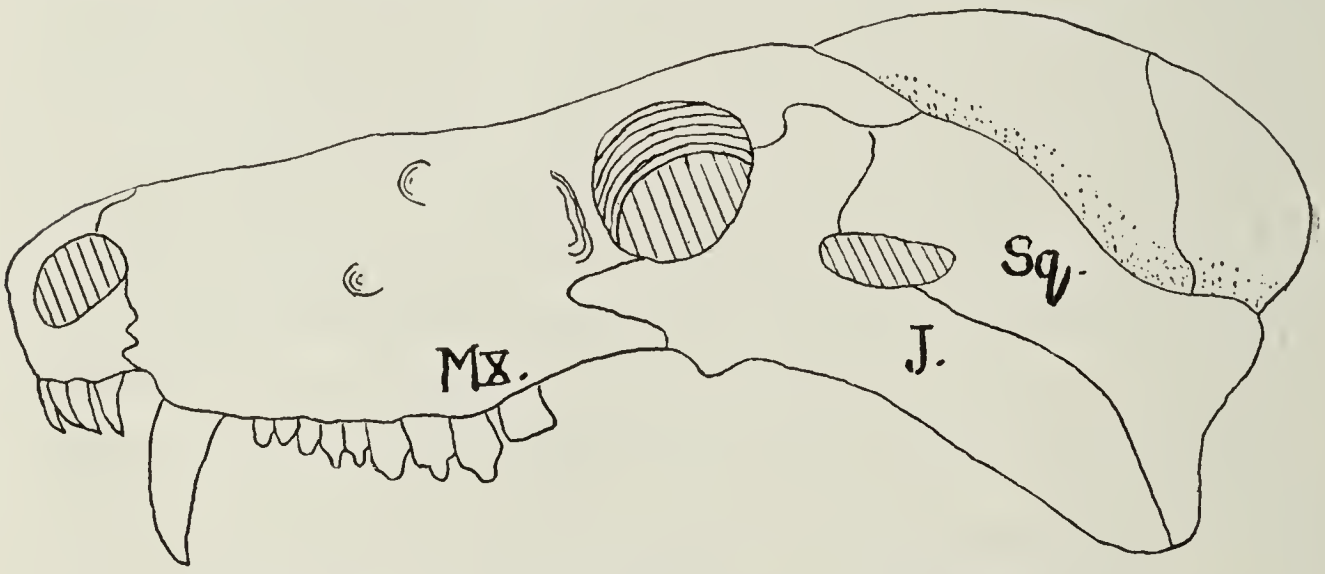

FIG. T. — Lateral view of the skull of Cynognathus, after Woodward. *J.*, jugal; *Mx.*, maxillary; *Sq.*, squamosal.

persists in these orders. Evidently this was Cope's ('92) conclusion although he calls that element the supratemporal.

Broom (:01, p. 182) and Williston (:04) state that these orders possess the most medial only of the bones of the temporal region of the Cotylosaur skull and that the two other elements have disappeared. It is evident that they correctly homologized the bone in question with the mammalian squamosal but since in other reptiles they gave the name squamosal to the medial element of the three, they found it necessary to assume that their prosquamosal (squamosal proper) and the quadratojugal had disappeared, which involves the difficulty of making the upper element (my supratemporal) assume the primitive relations of the elements which have been lost. Baur ('94) supposes (and in this he is followed by Woodward, '98, and Osborn, :03) that the squamosal is really a complex of squamosal and supratemporal (prosquamosal), but this conclusion is wholly hypothetical and has no evidence to support it.

Summary.

The development of the mammalian squamosal shows it to be a membrane bone which overlies the otic capsule and is at first intimately connected with the incus (quadrate) by a dense and fibrous stroma. Its dorsal margin is widely separated from the lateral border of the parietal, and only late in development comes into juxtaposition with the latter. Hence, it must be concluded that close association with the quadrate (incus) and otic capsule is the primitive relation of the squamosal, and, therefore, the most important criterion in ascertaining its homology in the non-mammalian vertebrates. Juxtaposition with the parietal, on the other hand, is a relation which has been secondarily acquired, and one which has lead to erroneous views of homologies in the non-mammalian vertebrates.

Moreover, we find in certain fossil vertebrates (Stegocephala) which in all probability directly or indirectly gave origin to the Mammalia, not only the bone which corresponds perfectly with the squamosal as above defined, but a second bone also overlying the otic capsule between this squamosal and the parietal,— that is, in the interval which in the embryonic mammalian skull is unoccupied by bone. Hence, it seems reasonable to conclude that, in the phylogenetic development of the Mammalia, this bone which may properly be called the supratemporal, has been lost, and its place has been bridged secondarily by the upward development of the squamosal.

No bone has been found in the temporal region of the Caecilian skull homologous with the mammalian squamosal. The bone often so called, corresponds, in the author's opinion, more closely to a postfrontal.

In the Urodelan skull, however, there is a bone which develops in membrane, and overlies the quadrate and otic capsule, secondarily reaching the parietal. This is the squamosal.

As already stated there are two bones in the temporal region of the Stegocephalian skull external to the parietal. The more lateral, from its relation to the quadrate, the otic capsule, and the jugal, I have identified as the squamosal. The more median is the supratemporal. Hence an inversion of the names of these two bones as ordinarily used, is necessary. This is also in accord with the priority of use of these terms.

In the skulls of the Theriodontia, the Anomodontia, and the Sauropterygia the squamosal is the only bone which invests the temporal region.

The squamosal of the most primitive reptiles, the Cotylosauria, shows practically the same relations as that of the Stegocephala.

In the Ichthyosauria the squamosal covers the dorsal external surface of the quadrate, and articulates anteriorly with the postorbital, laterally with the quadratojugal, and dorsally with the postfrontal and supratemporal.

Comparison of the skulls of Sauranodon, the Pelycosauria, Stenometopon, Palaeohatteria, and Sphenodon leads to the conclusion that in the phylogenetic development of the last genus the supratemporal has been lost, and the bone which remains is the squamosal, its connection with the parietal being correlated with the disappearance of the supratemporal.

In Sceloporus the squamosal consists of two parts, an anterior process which articulates with the postorbital and jugal, and a posterior portion which develops in membrane upon the otic capsule and overlaps the dorsal extension of the quadrate. The supratemporal has undergone marked reduction which seems true of the Lacertilia as a class. In the fossil forms, Platycarpus and Liodon, the relations of the squamosal are practically the same as in the Lacertilia.

The single bone existing in the temporal region of the Ophidian skull has the same development as the supratemporal of the Lacertilia and cannot be called the squamosal.

In the Crocodilia we find a bone which develops in membrane upon the otic capsule and overlaps the dorsal extension of the quadrate, eventually occupying the postero-lateral superior angle of the skull. This is evidently the squamosal. The supratemporal is lacking, at least no embryological evidence has yet been produced as to its existence.

In the Dinosaurian skull it seems very probable that the supratemporal is lacking and the bone which adjoins the parietal and extends more or less ventrally alongside the quadrate, is the squamosal.

The term 'paraquadrate' introduced by Gaupp, and since adopted by several authors, is unnecessary, since (if we adopt the incus = quadrate homology), that bone of the Urodelan skull which Gaupp and his followers call the paraquadrate, agrees perfectly with the mammalian squamosal, and should be so named. Moreover, Owen's

term 'prosquamosal' which has been used by several American students, is also a synonym of squamosal and consequently should be discarded.

This research was carried on in the Biological laboratories of Tufts college during the year 1904–05 under the direction of Prof. J. S. Kingsley, and it gives me pleasure to acknowledge my indebtedness and gratitude to him for many valuable suggestions received during the work.

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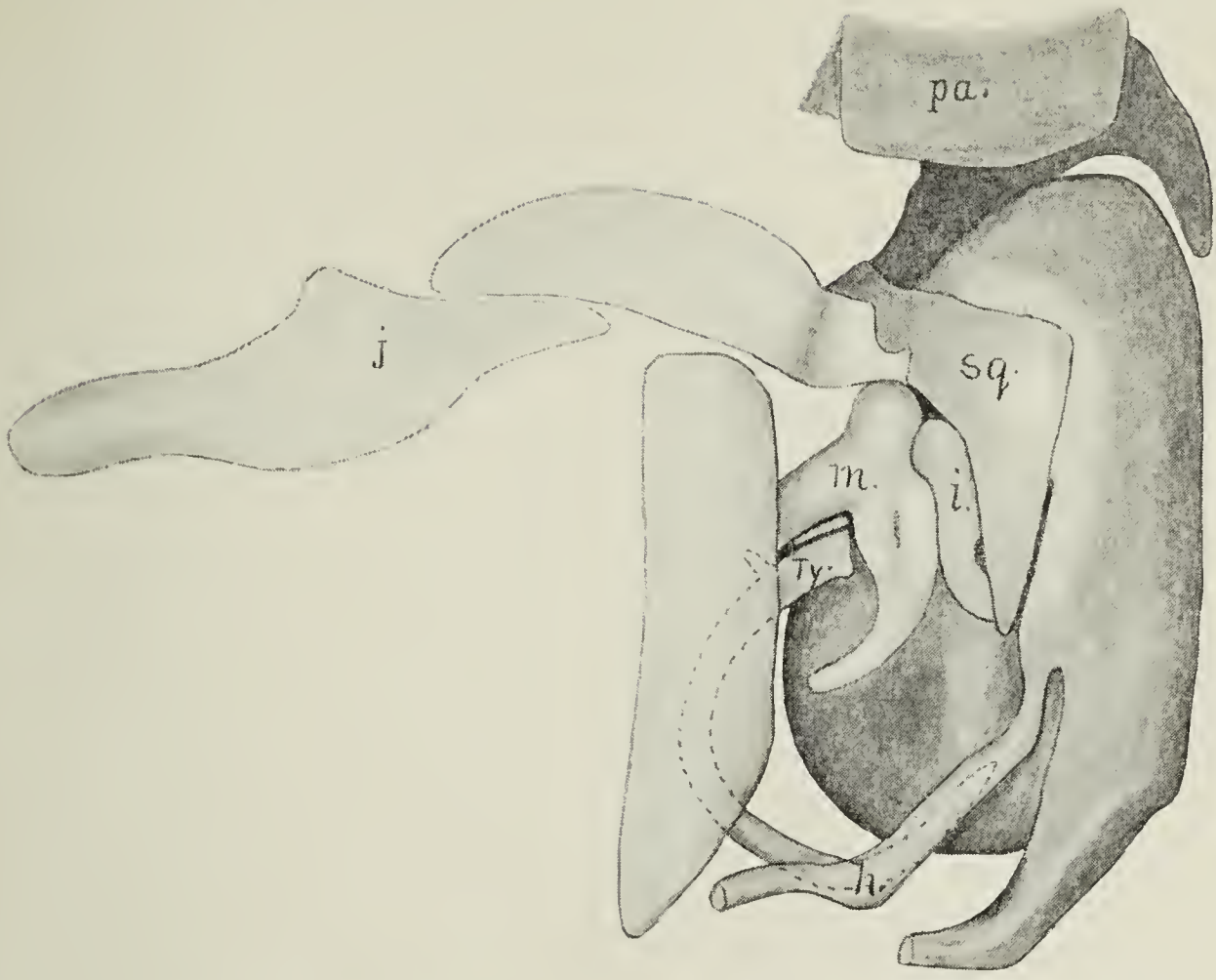
EXPLANATION OF PLATES.

PLATE 39.

Fig. 1. Reconstruction of the temporal region of the skull in a pig of 72 mm. *h.*, hyoid; *i.*, incus; *J.*, jugal; *M.*, malleus; *Pa.*, parietal; *Sq.*, squamosal; *Ty.*, tympanic.

Fig. 2. Transverse section of the otic region of a pig of 72 mm., showing the close relation of the squamosal to incus. *Em.*, external meatus; *fr.*, fenestra rotunda; *h.*, hyoid; *i.*, incus; *M.*, malleus; *Pa.*, parietal; *Sq.*, squamosal; *St.*, stapes; *tc.*, tympanic cavity; *VII*, facial nerve.



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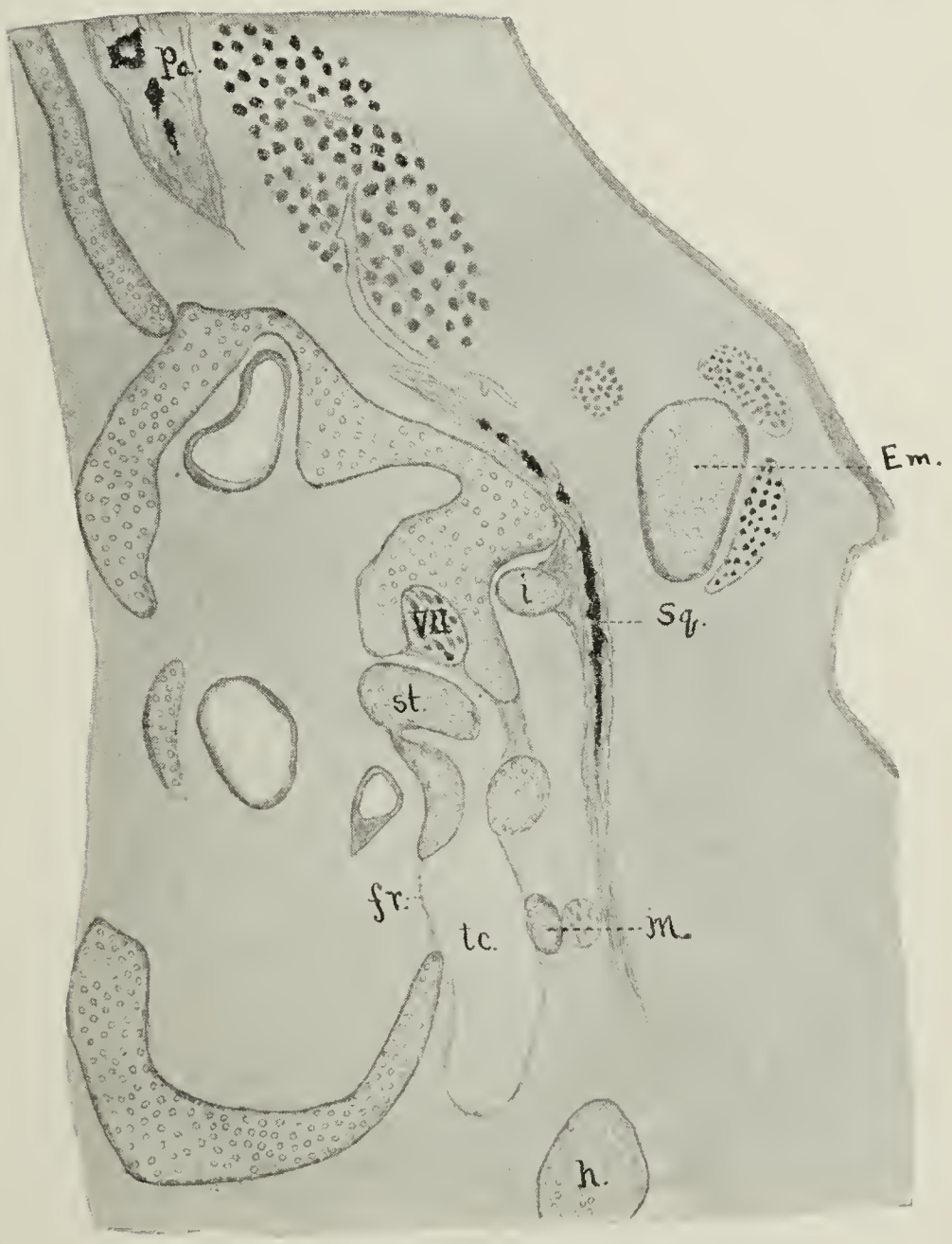

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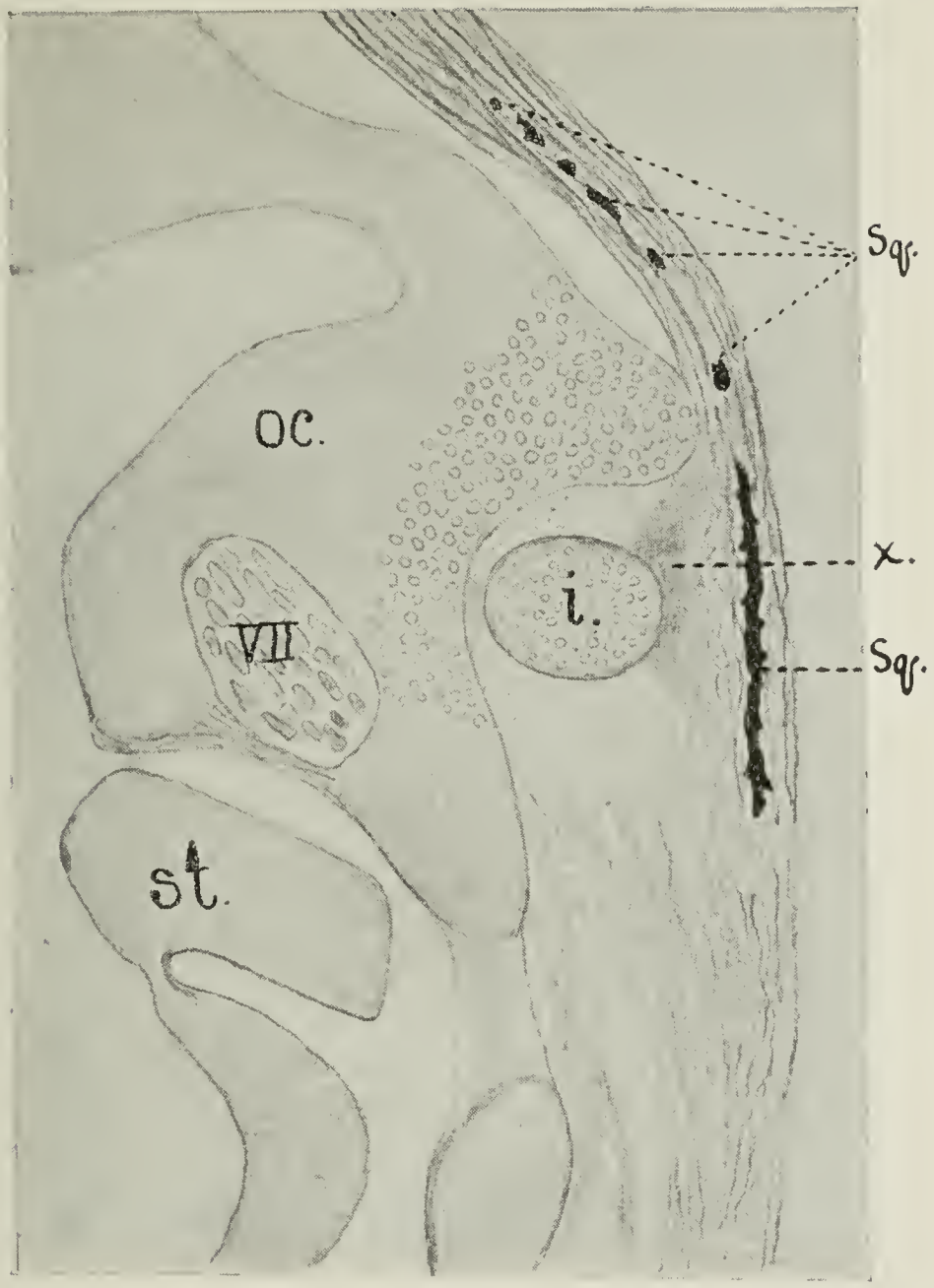
PLATE 40.

Fig. 3. An enlarged portion of Fig. 2, showing the dense stroma connecting the squamosal and the incus. *i.*, incus; *OC.*, otic capsule; *Sq.*, squamosal; *St.*, stapes; *x*, dense stroma; *VII*, facial nerve.

Fig. 4. Reconstruction of the temporal region of the skull in Amphiuma. *OC.*, otic capsule; *Pa.*, parietal; *Qu.*, quadrate; *Sq.*, squamosal; *Stp.*, stapes.



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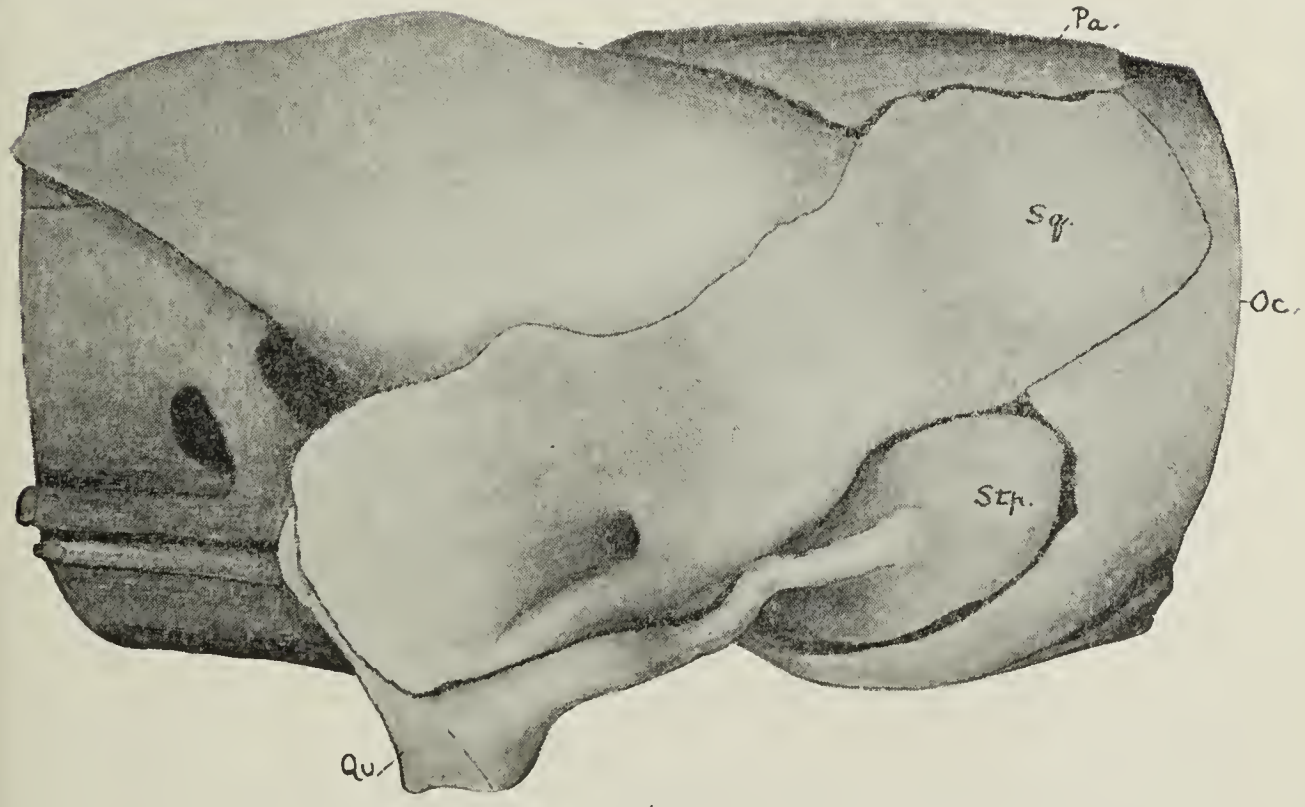

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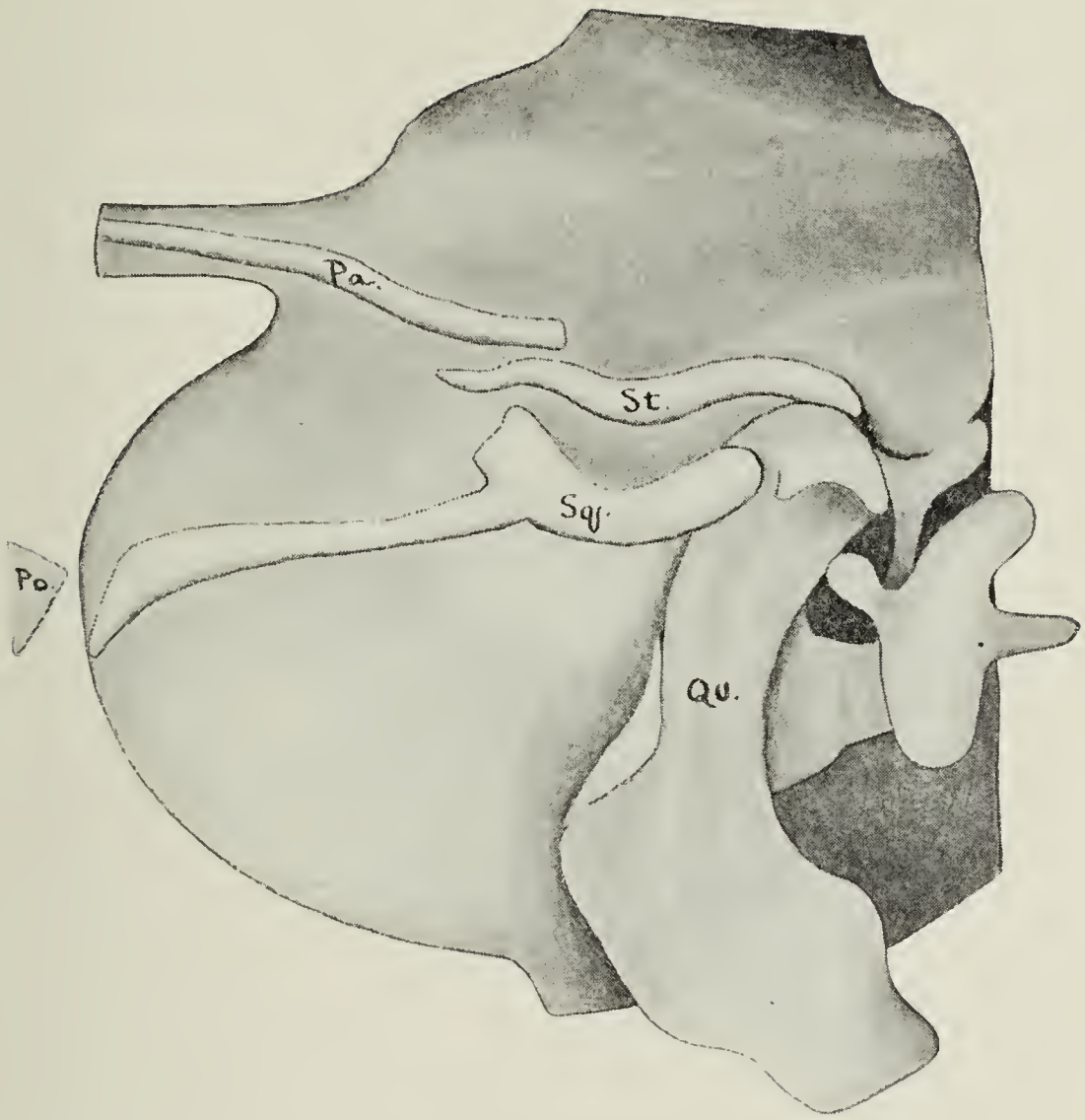
PLATE 41.

Fig. 5. Reconstruction of the otic region of young Sceloporus, showing the early development of the supratemporal and squamosal bones. *Pa.*, parietal; *Po.*, postorbital; *Qu.*, quadrate; *Sq.*, squamosal; *St.*, supratemporal.

Fig. 6. Lateral aspect of the skull of adult Sceloporus. *J.*, jugal; *Mx.*, maxillary; *Pa.*, parietal; *Po.*, postorbital; *Qu.*, quadrate; *Sq.*, squamosal; *St.*, supratemporal.



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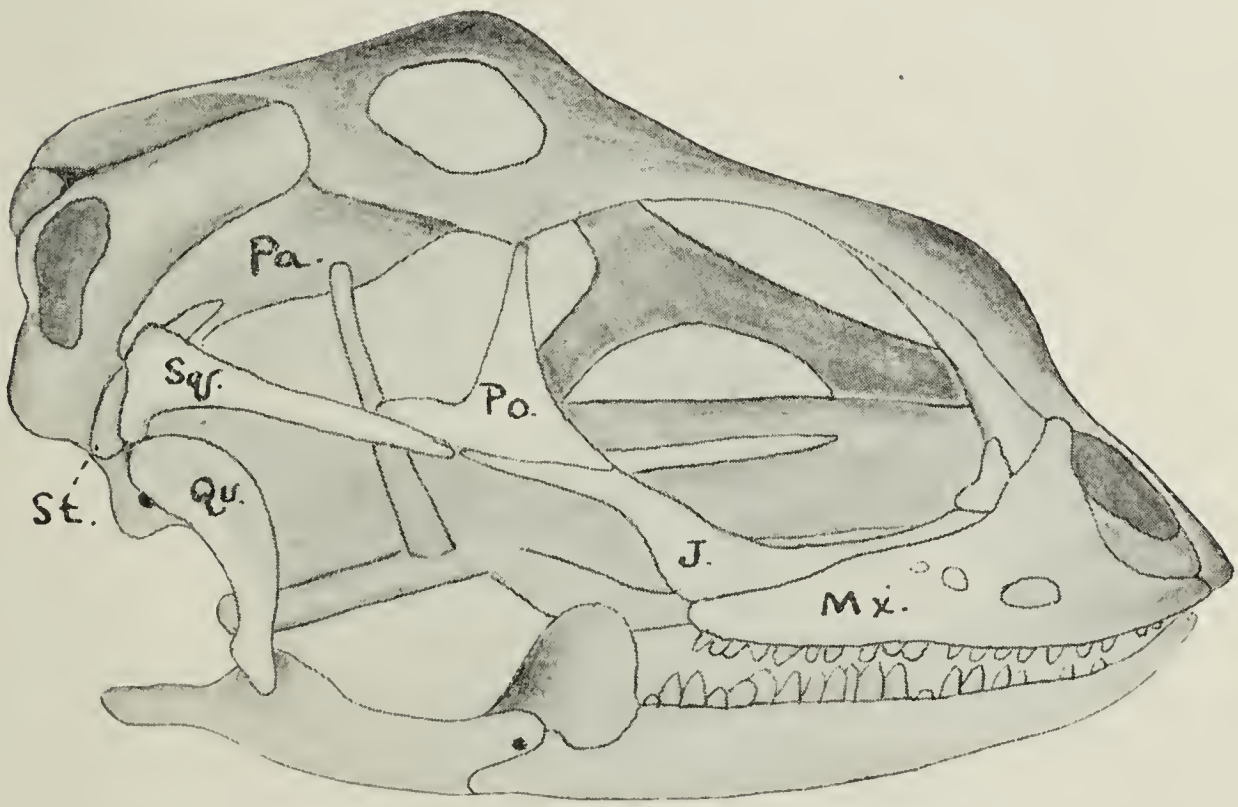

6

Tables showing interpretations by several authors of the bone which I would call squamosal.

DINOSAURIA.	CROCODILIA.	LACERTILIA.	RHYNCHOCEPHALIA.	ICHTHYOSAURIA.	COTYLOSAURIA.	SAUROPTERYGIA.	ANOMODONTIA.	THERIODONTIA.	MAMMALIA.	URODELA.	STEGOCEPHALA.	
											Squamosal, '86.	AMMON.
Squamosal, '91.		Squamosal, '86. Quadratojugale, '89. Prosquamosal, '94.	Squamosal and Supratemporal.	Squamosal, '87.		Squamosal and Supratemporal (Prosquamosal).	Squamosal and Supratemporal (Prosquamosal).	Squamosal and Supratemporal (Prosquamosal).			Squamosal, '86. Prosquamosal, '94.	BAUR.
			Prosquamosal, '99.									BAUR and CASE.
			Squamosal.								Squamosal.	BOULENGER.
					Squamosum, :04.						Squamosum, :04.	BROILI.
						Squamosal.	Squamosal.	Squamosal.				BROOM.
											Äusseres Paukenbein, '49.	BURMEISTER
			Prosquamosal, '98.									CASE.
Supramastoid, '92.	Squamosal, '71. Supramastoid, '92.	Squamosal, '71. Supratemporal, '92.	Supratemporal, '92.	Supratemporal, '92.	Supratemporal, '92.	Supratemporal.	Supratemporal.	Supratemporal.	Squamosal.	Squamosal, '71.	Supratemporal, '92.	COPE.
			Squamosal, '81-'89								Supratemporal.	CREDNER.
	Mastoïdien.	Temporal.		Temporal.					L'écailleuse et zygomatique, '25.	Tympanique.		CUVIER.
										Temporo-mastoïdien, '35.		DUGÈS.
										Paraquadrate, :05.		EMERSON.
				Supratemporale, 91.							Supratemporale, '89, '91.	FRAAS.
											Supratemporal, '83.	FRITSCH.
Squamosal, :01.	Squamosal, :01.	Supratemporal, :01.	Squamosal, :01.	Supratemporal, :01.			Squamosal, :01.	Squamosal, :01.	Squamosal, :01.	Squamosal, :01.	Supratemporal, :01.	GADOW.
	Squamosum, '94.	Paraquadrate, '94.	Paraquadrate, '94.						Squamosum.	Paraquadrate, '94.	Paraquadrate, '94.	GAUPP.
	Squamosum, '98.	Quadratojugale.	Squamosum, '98.						Squamosum.	Tympanic, '78, Squamosum, '98.		GEGENBAUR.
			Mastoid, '67.									GÜNTHER.
	Squama temporalis.	Quadratojugale, '37.							Squama temporalis, '37.	Tympanicum, '37.		HALLMANN.
										Squamosal.		HASSE.
										Squamosal, '90.		HAY.
	Squamosum, '90.	Squamosum, '90.	Squamosum, '90.							Tympanicum, '74.	Tympanicum, '74.	HOFFMANN.
		Quadratojugal.										HOLLAND.
			Sqamosal, :01.									HOWES and SWINNERTON.
	Squamosal, '71.	Squamosal, '71.	Squamosal, '71.	Supratemporal, '71.					Squamosal.	Squamosal, '74.	Supratemporal, '71.	HUXLEY.
									Squamosum, 1670.			KERCKRINGIUS.
										Squamosal, :03, :05.		KINGSBURY.
			Temporal, '92.									LORTET.
Squamosal, '96.												MARSH.
											Supratemporal, '73.	MIALL.
Squamosal and Prosquamosal.		Prosquamosal, :03.	Squamosal and Prosquamosal.	Prosquamosal, :03.	Prosquamosal, :03.	Squamosal and Prosquamosal.	Squamosal and Prosquamosal.	Squamosal and Prosquamosal.			Prosquamosal, :03.	OSBORN.
	Mastoid, '66.	Zygomatique. '39. Squamosal, '66.		Squamous [1] Element of Temporal, '39.		Squamosal, '60.	Squamosal, '76.				Supertemporal. Supersquamosal, '60.	OWEN
	Squamosal.	?							Squamosal.	Squamosal.		PARKER.
	Squamosal, '77.	Squamosal, '77.							Squamosal, '77.	Squamosal, '77.		PARKER and BETTANY.
			Squamosum, :00.									SCHAUINSLAND.
				Supraquadrate, '80.			Sqamosal, '89.				Supraquadrate, Supratemporal, '89.	SEELEY.
		Squamosum, '92.	Supratemporale, '93.									SIEBENROCK.
	Mastoideum, '46. Squama temporalis, '56.	Quadratojugale, '46. Squama temporalis, '56.								Tympanicum, '56.		STANNIUS.
		Quadratojugale.								Tympanic, '77. Squamosum, '93. Paraquadratum, :06.		WIEDERSHEIM.
Squamosal, :04.	Squamosal, :04.	Prosquamosal, :04.	Quadratojugal (Dimetrodon) Squamosal.	Prosquamosal, :04.	Prosquamosal, :04.	Prosquamosal, :04.	Squamosal, :04.	Squamosal, :04.			Prosquamosal, :04.	WILLISTON.
Squamosal, '98.	Squamosal, '98.	Squamosal, '98.	Squamosal, '98.	Supratemporal, '98.	Supratemporal, [2] '98.	Squamosal, Supratemporal, and Quadratojugal, '98.		Squamosal and Supratemporal, '98.			Supratemporal, '98.	WOODWARD.
Squamosum.	Squamosum.	Squamosum.		Supratemporale.			Squamosum.			Squamosum.	Supratemporale.	ZITTEL.

[1] Other terms of Owen: Supersquamosal, '60, Supratemporal, '60, and Prosquamosal, '65-'81.
[2] Pareasauria = Cotylosauria.

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THE ANNULUS VENTRALIS.

By E. A. Andrews.

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No. 12.— THE ANNULUS VENTRALIS.

BY E. A. ANDREWS.

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Introduction.

Of the nine genera of crayfishes only one — Cambarus — is known to have the peculiar organ called by Hagen the annulus ventralis. In this genus there are some sixty-six species, as compared with about forty-four species in all the other genera, and each species is thought to have its peculiar specific form of annulus ventralis.

The crayfishes of the genus Cambarus are widely scattered over North America east of the Rocky Mountains and occupy this large area to the exclusion of all other crayfish except for a very few species of Astacus which extend from the west of the above mountain range some distance to the east.

The discovery of the annulus ventralis and its utilization as a specific character was first made by Hagen ('70), but its physiological value escaped him, as was almost necessary, for he says: "I have not seen living specimens" ('70, p. 16). The annulus is found in the female crayfish only and Hagen thought it fit for some sexual purpose and likely to be used for secretion, possibly, but not probably, for gluing the eggs to the abdominal appendages.

The figures and descriptions given by Hagen and by subsequent authors who have made use of the annulus as a specific character (Faxon, '85, '98; Hay, '96), show only the form of the external protuberances and depressions and sutures of a specialized area of the shell and give no idea of its internal structure, except in the first case, that of Hagen, whose figure of the internal side of the shell is inadequate and whose description is but brief and fundamentally erroneous. When therefore it was observed (Andrews, '95) that this organ is used as a sperm receptacle into which the male puts the sperm that is subsequently to fertilize the eggs, its great importance as a necessary link in the chain of reproductive organs, as an organ whose absence would lead to the extermination of all the Cambarus crayfish, seemed to demand a more thorough examination of its structure.

In fact the annulus is here claimed to be one of those remarkable

organs used in cases of *indirect sperm transfer*. That is, one of those exceptional cases met with here and there in several of the large groups of animals, in which the sperm is neither set free in water nor transferred into the egg-discharging passages by an intromittent organ.

In the following pages the anatomy and use of the annulus will be described more in detail than has been done hitherto though a preliminary account was published elsewhere (Andrews, **:05**).

Description.

Structure in Cambarus affinis.— Externally the annulus ventralis appears as a part of the shell, or exoskeleton, on the ventral side of the female thorax. It is a transversely elongated, elliptical plate, lying across the middle of the body in the interval between the two special sternal plates that lie between the bases of the fourth pair of legs and between the bases of the fifth pair of legs.

In text-figure A the bases of the 2, 3, 4, and 5 pairs of legs with the sternal plates between them are shown and also the small first pair of abdominal appendages. On the bases of the third legs are the two large elliptical openings of the oviducts; posterior to these the wide, concave sternal plate between the bases of the fourth legs; and crowded close against this is the annulus bearing two marked protuberances and a deep transverse depression bounded posteriorly by an elevated rim. Posterior to the annulus, the narrow sternum between the fifth legs bears an elevated transverse ridge that will subsequently be referred to in attempting to explain the way in which the sperm is discharged from the cavity of the annulus.

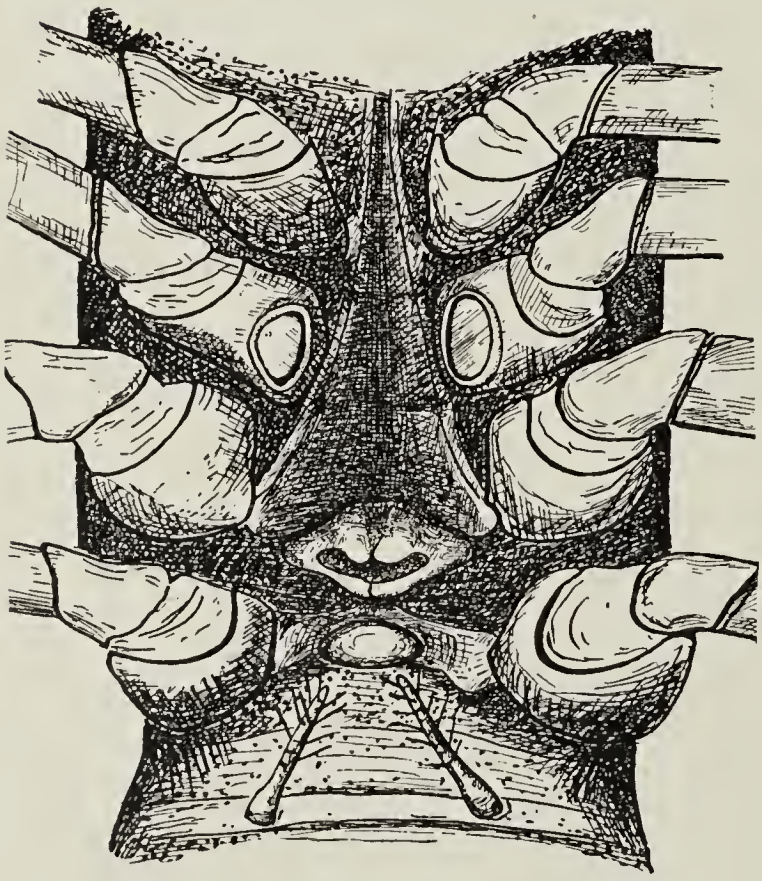

Fig. A.

The annulus is thus separated from the openings of the oviducts by the entire length of the sternum of the region bearing the fourth legs.

The exoskeleton of the annulus is so thick and rigid that it cannot readily be bent, while the exoskeleton just next to it posteriorly and on each side is thin and pliable. Anteriorly the annulus is rather firmly fastened to the thick sternal plate between the fourth pair of legs by somewhat thinner exoskeleton that acts like a leather hinge so that when pressure is exerted upon the annulus it may be raised from a horizontal position into a much inclined one, somewhat like a trap door. This up and down motion is rendered possible by the pliable, thin, exoskeleton posterior to the annulus and anterior to the stiff part of the sternum between the fifth legs.

By cutting through the thin parts of the exoskeleton posterior to the annulus and on each side of it and by cutting the stiff hinge-like connection of annulus and sternal plate anterior to it, the entire exoskeleton of the annulus may be removed with some little injury to the underlying tissues of the annulus.

A more detailed view of such a severed annulus exoskeleton as seen from the ventral and somewhat from the posterior points of view is generalized in figure 1 (pl. 43), since each specimen presents slight differences in ratio of transverse to longitudinal diameter, in size and shape of protuberances and depression, and in amounts of curvature of different regions.

Each annulus presents two large subcentral, tuberosities anterior to a deep transverse depression which is bounded posteriorly by an elevated rim. On the median plane this rim juts out anteriorly into the depressed area as a bent ridge which we will speak of later as the promontory. Along this ridge is a sharp groove, or suture, which leaves the median plane and passing down to the right along the promontory suddenly turns to the left, on a low level, and crossing the median plane, ends in a narrow opening more or less concealed by the overhanging tuberosities. This opening, or orifice, is on the left of the median plane and is somewhat overhung both by the large tuberosity on the left and by a transverse spur from the large tuberosity on the right. This transverse spur is a prolongation of the right tuberosity crossing the median plane and ending more or less under the edge of the left tuberosity. Anteriorly the annulus shows a wide median groove between the anterior faces of the large tuberosities. The

generally elevated character of all the central part of the annulus is well shown from an anterior view (pl. 43, fig. 4), where the two tuberosities are seen as elevations above the general level and the edge is everywhere much lower. The edge in the foreground was the hinge-like connection of the annulus to the sternal plate between the fourth legs. On the median plane an anterior valley-like groove rises up between the anterior faces of the tuberosities and ends abruptly where the transverse spur passes across from the left tuberosity (the right of figure 1) to end beneath and somewhat posterior to the other great tuberosity.

The chitinous exoskeleton above represented is dense and hard with a smooth surface slightly marked by wrinkle-like lines but free from setae. Posteriorly it is more or less calcified. In life the tuberosities are somewhat yellowish or reddish while the posterior rim and promontory are white or bluish so that in a photograph taken with a non-orthochromatic plate the tuberosities are dark and appear as depressions while the rim appears light and as if much elevated.

In cutting out the annulus exoskeleton from a living crayfish there is some removal of underlying tissue which adheres to the dorsal side of the exoskeleton and must be removed to gain a clear view. Such a dorsal view of the exoskeleton merely is shown in figure 2 (pl. 43) which is the reverse of the same specimen shown in figure 1. From the outside the entire annulus plate is elevated and has a low bounding edge (pl. 43, fig. 1), from the inside view it is depressed and has an elevated bounding edge (pl. 43, fig. 2). The bottom of the dish-like annulus as now seen shows anteriorly two very deep pits that correspond to the tuberosities and posterior to these are elevated transverse regions corresponding to the transverse depression of the outside view. Thus the external protuberances and depressions are represented by their negatives on the dorsal aspect and the sculpturing of the annulus is obtained not so much by thickening of solid exoskeleton as by a *repoussé* in and out bending of the exoskeleton to fit, as we shall later see, over corresponding foldings of the living epidermis. But the most marked feature in the dorsal view is a bent longitudinal rounded ridge. This rises anteriorly just behind a median elevation between the pits of the tuberosities, a median elevation corresponding to the anterior median depression of the ventral view (pl. 43, fig. 1). The bent ridge then passes to the right and, enlarging, passes to the left, then diminishing, passes to the right, and near the median line

disappears posteriorly in the deep transverse groove that represents the elevated transverse rim of figure 1. The bent ridge thus follows in general the course of the zigzag suture seen on the ventral side as passing from the anterior orifice to the posterior ending of the suture upon the posterior rim. The amount of protuberance of this ridge is variable, but in general a posterior view of the annulus exoskeleton, as in figure 3 (pl. 43), shows the ridge as a transverse mass projecting above the rim of the annulus. In this view the high, sheer, posterior face of the annulus with its slight median groove, ends below in a sharp edge where the exoskeleton was cut off from the thin membrane posterior to the annulus. The mass below this is the above curved ridge while the two dark masses above are the two tuberosities in the background, the ventral side being uppermost.

When the annulus was removed and dried with filter paper and the ridge broken open it was found to be a hollow structure having a thick, brittle wall and a cavity lined by a thin, smooth, yellow, chitin-like layer.

When the exoskeleton of the annulus was made translucent, the true form of this curved ridge, that projects dorsally from the rest of the exoskeleton, was seen to be that of a tube or trumpet, with a wide mouth anteriorly and a small closed tip posteriorly. Such a translucent annulus (pl. 43, fig. 5) seen from the ventral side shows the posterior rim and promontory and the posterior borders and the spur of the tuberosities of figure 1 as more opaque regions in a generally clear field and in addition the dorsal ridge showing through the translucent ventral exoskeleton as a bent, hollow tube with very thick walls. The central cavity of the bent tube opens anteriorly on the left by a curved orifice partly overhung by the left tuberosity and the transverse spur of the right tuberosity. From the orifice the cavity may be seen passing to the right, then backward and to the left, finally to end in a small median enlargement lying above the middle of the promontory. As shown in the figure the curve of the tube is like that of the zigzag suture seen on the surface, but the suture does not exactly overlie the cavity of the tube; it is short and angular while the cavity of the tube is long and sinuous.

The dorsal ridge of the annulus is thus like a trumpet. We will speak of its transverse anterior part as the vestibule opening to the left by a somewhat crescentic orifice, at the bottom of the transverse depression of the annulus. The cavity following the vestibule is the

narrow bent tube we will call the trumpet tube and the small rounded posterior sac that ends the cavity will be called the recess. In a stained frontal section of the exoskeleton of the annulus (pl. 43, fig. 6) the very thick walls of the trumpet have an inner lining of chitinous material, not here seen, and are made of an inner darkly stained layer and a thick outer layer. This outer layer on the level of this particular section is continuous right and left with the material of the bottom of the transverse depression of the annulus, while anteriorly it is continuous with the material that forms the rim all round about the annulus. The two large spaces right and left are the portions of the annulus that descend as the cavities within the tuberosities and they are filled by connective tissue and lined by epidermis. This is also true of the small median space posterior to the trumpet cavity in the figure. This space is the deepest part of the posterior transverse groove of figure 2 (pl. 43), that is, part of the promontory of figure 1. The trumpet cavity in figure 6 (pl. 43) shows anteriorly the wide vestibule passing from left to right and then the narrow and bent tube which in this section ends abruptly but in lower sections was followed downward as the terminal enlargement or recess.

The cavity of the trumpet is thus bent not only from right to left but up and down in a vertical plane so that the posterior termination is much below its general course, as is well seen in text-figure B. This is a view of a median vertical section through the entire annulus and the parts anterior, posterior, and dorsal to it. The exoskeleton is represented in black and the part of it belonging to the annulus is the downward projecting part containing three small holes, two of which open below to the exterior by slits. Dorsal to the exoskeleton is a mass of connective tissue, full of cavities, in life containing blood, and this connective tissue is everywhere covered by epidermis where it comes near the exoskeleton. Passing from side to side in the figure is the part of the slender sternal artery and this is connected with the descending artery near the middle of the figure. This descending artery is slightly indicated passing up to the right of a large venous space. Most dorsally in the figures are the median nerve-cord and the ganglia of the second, third, and fourth somites of the thorax (counting from anterior which is right in the figure) and the ganglion of the fifth thoracic somite, lying far to the left in the figure. It will be seen that the nerve cord connecting the ganglion is interrupted where the descending artery and vein pass, and other sections show the nerve-cord as a ring around these vessels.

The annulus is all the protuberant mass of connective tissue and epidermis covered by exoskeleton that lies just below the sternal artery where the above nerve ring exists, that is, where the descending artery passes forward and backward as the sternal artery. It will be seen that the exoskeleton runs in and out over the protuberances and depressions formed by the connective tissue and epidermis. The larg-

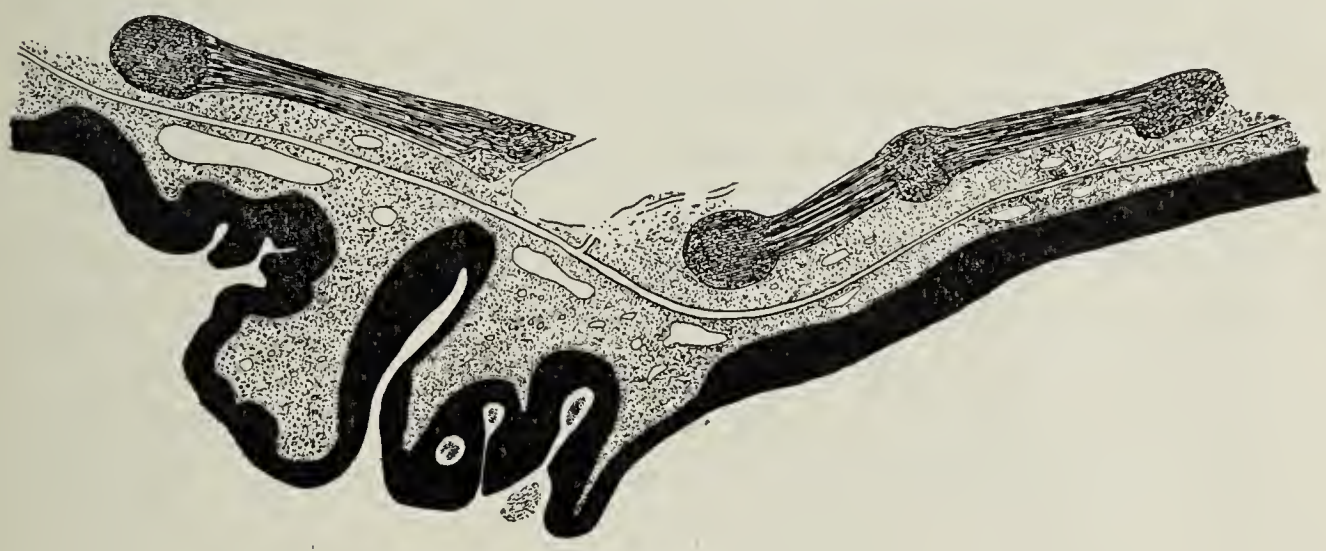

FIG. B.

est protuberance here shown is the annulus; the other large protuberance, to the left in the figure, is the ventral transverse ridge shown in text-figure A posterior to the annulus and between the fifth legs. On the right of text-figure B is the very thick exoskeleton that forms the bottom of the sternal groove all along the second, third, and fourth somites as seen in text-figure A. Where this median exoskeleton suddenly becomes thin in section, text-figure B, is the hinge-like anterior border of the annulus. In like manner where the very thick exoskeleton on the anterior face of the sternal ridge of the fifth somite becomes thin, it passes over into the posterior edge of the annulus.

In removing the annulus to gain such views as figures 1 to 5, in plate 43, the exoskeleton is cut across the two thin regions shown in text-figure B. A horizontal cut through these thin places removes the annulus as a *truncated cone* of connective tissue covered by epidermis and exoskeleton. In this exoskeleton is a cavity so sinuous as to be cut in three places in the above figure. Such a cut leaves behind on the animal a bleeding surface of connective tissue close under the sternal artery, and the edges of this wounded surface are formed by exoskeleton overlying epidermis.

The three cavities in the thick exoskeleton of the annulus as repre-

sented in text-figure B show not only that the trumpet cavity winds from side to side but that the part to the right, the anterior vestibule, is more dorsal than the part to the left, the posterior recess or terminal sac. It also shows that the cavity of both vestibule and trumpet tube opens out to the exterior by narrow slits. The same can be shown to be true of the recess in certain planes. The granular material indicated in these cavities of the annulus was sperm while the granular mass just external to the annulus and ventral was part of the sperm-plug, that is, the wax-like mass protruding from the orifice.

The general character of the annulus and adjacent organs is again shown in text-figure C which is a cross section but not quite vertical. Above, it shows the large muscle masses right and left of the ventral nerve-cord which is cut across the long commissure between the ganglia of the fourth and fifth thoracic somites.

Below the nerve-cord is the small sternal artery embedded in connective tissue which forms the general mass of the annulus. The

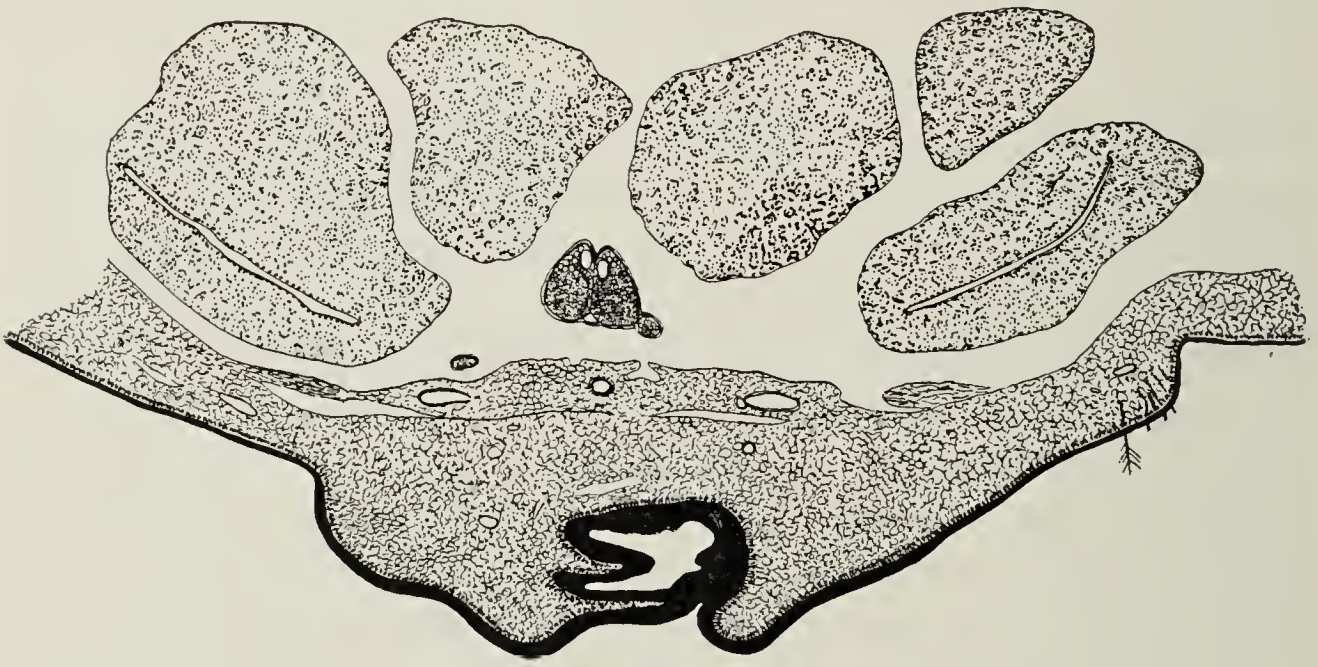

Fig. C.

annulus is the large mass of connective tissue projecting downward and covered by exoskeleton that thins off right and left into the thin exoskeleton of the non-elevated surface of the body. This thin lateral exoskeleton is easily cut to remove the annulus as a conical mass. In the middle of the annulus is a large cavity with very thick exoskeletal walls; this is the vestibule of the trumpet and its irregular form is due to the fact that it is cut anteriorly, and somewhat obliquely from side to side. The exterior depression beneath this cavity is the anterior

median groove seen in figure 1 (pl. 43), and the two elevations right and left of it are the tuberosities in nearly vertical section. The transverse bridge that lies between the cavity of the vestibule and the exterior in this section, text-figure C, is a section of the spur seen in figures 1 and 5 (pl. 43), passing over from the right tuberosity to end under the left tuberosity.

The actual orifice leading from outside into the vestibule of the trumpet is variable and also difficult to see on account of the overhanging of the tuberosities and the spur. As indicated in white in figure 7 (pl. 43) it is a crescentic aperture with its concave side more or less encroached upon by the spur from the right tuberosity. The large cavity of the vestibule is there represented by the long light area leading off from the crescentic orifice to the right. The dark line bounding the orifice in the figure represents the optical section of the chitinous covering of the exoskeleton which dips in at the orifice to line the interior of the whole trumpet. To the right this dark bounding line is continued to represent the commencement of the zigzag suture.

The cavity of the trumpet communicates with the surface not only by the above open orifice but by a continuous bent slit that comes to the surface as the above zigzag suture represented in figures 1 and 5 (pl. 43). The sides of this slit are so nearly in touch with one another and the suture is so nearly a closed one that this long continuous opening of the trumpet can be made out only with difficulty in the natural state though in dried and shrunken section material it is quite evident. The nature of this connection of cavity and surface may be made out from such sections as figures 11 and 14 (pl. 44). The former represents a vertical longitudinal section much like that shown in the central part of text-figure B. The ventral side is uppermost and the anterior face is the sloping one on the right. The cavity is cut across as four spaces and in three of these there is patently a slit leading out to the surface, but the fourth, most to the left, is the most ventral terminal pouch or recess and it opens into a common slit leading to the surface from the third space. The bounding dark line represents the clear chitinous layer that covers the entire exoskeleton and passes in at each slit to line all the internal cavities in the exoskeleton of the annulus. The more vertically striated, external layer of the exoskeleton is continued as the striated lining layer of the trumpet while the thicker inner laminated layer of the exoskeleton is continued as the

laminated outer part of the exoskeleton of the trumpet. Moreover, the epidermis which underlies and produces the exoskeleton continues inward to cover over the entire trumpet. Comparing this figure with text-figure C we may regard the trumpet as made by an inpushing of epidermis that has formed a very thick exoskeleton mass in its cavity. And this exsokeleton presents a deep narrow curved ditch enlarged at the bottom but with sides almost against one another and a very narrow opening to the surface. In all paraffin sections, even in those of an unused annulus from a female that had just cast its exoskeleton, the opening of the curved trumpet cavity to the exterior is an evident slit as in figure 11 (pl. 44); but a more natural condition is represented in very thick, free-hand sections of material cleared in oil of cloves as in figure 14 (pl. 44). This is a view from the left of a very thick section of a translucent annulus showing on the right the projecting tuberosity and on the left the posterior promontory, with their cavities not filled by connective tissue as they were in life. The large central mass is the trumpet projecting dorsally from the center of the annulus, the ventral side being above in this view. To the right, in the trumpet, is seen the vestibule in optical section, passing toward the observer and then sweeping away toward the left. Within this cavity is a composite mass of wax-like material. A narrow curved slit passes from the vestibule toward the left to end at the outer surface. A like curved slit passes from the surface to the elliptical cavity which is the bent trumpet cavity cut across nearly at right angles. Focussing proved that the two slits shown, were but parts of one continuous curved slit. Far to the left is the terminal recess full of sperms, indicated by dots. Some other sperms scattering out from the recess indicate a slit lying nearly in the plane of the section and leading from the posterior part of the trumpet and from the recess to the surface (compare fig. 11, pl. 44).

The lines along which the curved slits come to the surface are the successive parts of the zigzag suture seen on the surface in figures 1 and 5 (pl. 43), but this is readily demonstrable only from focussing such a preparation as that shown in figure 5. It is there seen that the zigzag suture is made up of three successive lines. The anterior one, formed where the edges of the orifice meet, passes to the right and posteriorly and runs beyond the second line which in turn slightly runs beyond the third line that ends the suture on the median plane. Focussing shows a curved slit passing from the first line forward and

dorsally as well as to the right to open into the vestibule and first part to the trumpet tube and a second curved slit passing dorsally in a curve chiefly to the right, to open into the posterior part of the trumpet tube, while a third slit from the median line passes dorsally a slight distance and has complicated relations to the recess, to be described below. The three slits are in reality but parts of one curved slit sinuously bent where opening into the trumpet dorsally and sharply bent in lines where coming to the surface as the zigzag suture. It must also be borne in mind that the suture, as shown in figure 1 (pl. 43), passes in a vertical curve over the promontory and then slantingly downwards to the left. Where the successive lines of the suture meet there are side puckerings of the suture, and there are other minor side folds.

Morphologically we may regard the trumpet as a sort of flat pocket folded from side to side and with its mouth represented anteriorly by a crescentic orifice and along the rest of the pocket by a nearly closed suture. The lining of this pocket is exoskeleton so thickened as to leave only a narrow, bent slit from the suture down to the rounded bottom of the pocket which thus becomes a partly shut off trumpet-like cavity.

But there is a peculiar complication at the posterior end of this morphological pocket and that is the recess above mentioned which in turn may be interpreted as side pouches from the main pocket. Owing to the number of curved spaces and their walls seen in transparent material and to the fact that continuous series of thin paraffin sections are difficult to obtain, much time was spent in arriving at a clear conception of this recess in this species of Cambarus.

The recess may be described as a lateral and posterior extension of the tip of the cavity of the trumpet, somewhat in the shape of a pair of saddle-bags. Seen from the ventral side (pl. 43, fig. 5), the recess appears as a rounded sac often full of sperm. When more magnified this mass of sperm looks somewhat heart-shaped (pl. 47, fig. 27). This figure shows the promontory in a transparent preparation of the specimen from which the section figure 14 (pl. 44) was subsequently cut. On the surface the posterior, middle, and part of the anterior lines of the zigzag suture are shown as lines bounded by opaque bands indicating the dipping in of the exoskeleton at the bottom of superficial grooves and the practically closed up state of the slits leading dorsally to the cavity of the trumpet. The posterior line of the suture passes beyond the heart-shaped mass of sperms both

posteriorly and anteriorly and any connection between it and the recess is not apparent. The cavity of the trumpet, represented as empty, seems to end bluntly just anterior to the sperm mass in the recess, though it also seems to run under the sperm mass. In the original preparation scattered specks indicated the curved slit leading from the middle line of the suture dorsally into the long curve of the trumpet on the extreme left.

Only when the sperm is absent and the suture cracked open by pressure or by drying does the true relation of suture, recess, and trumpet cavity become evident as in figure 10 (pl. 43). In this figure the curved surfaces passing from the suture to the cavity of the trumpet are represented by parallel rulings. Anteriorly the open suture is connected by a slit or curved passage with the parallel cavity above and to the left of it. The walls of the trumpet cavity are represented by a double line. This trumpet cavity then passes to the right across the suture and above it and curving posteriorly on the right side of the suture seems to end in part on the median plane just above the suture and in part as a blind in-pushing of the anterior wall of the heart-shaped recess. Thus the cavity of the trumpet lies far to the left of the suture in the anterior part of this figure and connects with it by a long plane or slit, then in crossing the suture, opens directly down into it for a short distance and afterwards goes some distance to the right of the suture and connects with it by a long curved opening or slit. At the posterior end the cavity, coming to the median plane again, opens directly down through the suture and it is here very near the ventral surface of the annulus. Dorsal to its opening into the suture, the cavity runs on posteriorly for a short distance above the recess as a blind sac; or one might say the cavity of the trumpet in passing ventrally toward the surface runs posteriorly farther than necessary and then turns anteriorly again to end just above the median suture. The part of the suture posterior to the tube of the trumpet is shallow and it would seem as if the heart-shaped recess were entirely cut off from the cavity of the trumpet by the transverse wall shown in figure 10 (pl. 43) crossing the suture. This, however, is not the case since this wall is some distance dorsal to the mouth of the suture as seen in figure 14 (pl. 44) where this wall shows as a nearly horizontal shelf jutting out between the sperm in the recess and the sperm in the terminal part of the trumpet tube.

The recess thus has a slight connection with the terminal part of

the tube over an oblique wall; it is also not a single horizontal space as indicated in figures 27 (pl. 47) and 10 (pl. 43) but it extends dorsally some distance as two pouches, one right and one left as is indicated in the vertical transverse section (pl. 43, fig. 8). This is cut across the promontory just where the tube ends above the recess. In the middle of the figure is shown the oblique ending of the tube and the bridge-like rim above, which, in figure 10 (pl. 43), seems to spring across the suture from side to side. Above this rim is the widely expanded recess opening, above in the figure, to the surface by a slit and, laterally, extending dorsally alongside of the tube termination for some distance as a blind pouch. The pouch on one side is larger than that on the other side.

This dorsal pouching of the recess leads to such appearances as shown in figure 20 (pl. 45) when the recess and terminal part of the tube are full of sperm. This is a horizontal section through the promontory and near the ventral surface. The tube is seen sweeping into a median position and blindly ending full of sperm cut off by thin lateral walls from the two large sperm masses which fill the pouches of the recess. In more ventral sections of this series the lateral pouches were continuous with one another and then had a common connection with the median tube over the rim shown in figures 8 and 10 (pl. 43) and 14 (pl. 44).

As seen in figure 10 (pl. 43) the median suture extends posteriorly much beyond the end of the trumpet tube; for a short distance this part of the suture connects by a slit with the recess as seen in figure 8 (pl. 43) and thus the recess could discharge both anteriorly over the rim into the end of the slit leading from the tube to the surface (pl. 44, fig. 14), and ventrally by its own slit direct to the surface. Soon, however, the median suture passes posterior to the recess and a very long stretch of it extends to the posterior border of the annulus without any connection with internal spaces. In section 16 (pl. 45) which is posterior to section 8 (pl. 43) the extreme posterior end of the recess is shown full of sperm as seen from the posterior face so that the bridge and end of the tube are faintly indicated in the thickness of the section. The sperm is seen passing somewhat upward toward the external suture through a bent imperfect slit. It seems that the slit is here only in part a natural slit lined by cuticle and from its bottom goes off to one side a mechanical break leading into the sperm mass. Still farther posteriorly (pl. 43, fig. 9), the suture has not even this arti-

ficial connection with the recess but opens only a short distance into the exoskeleton as a simple cleft from the bottom of which a faint useless crack leads dorsally. The small cavity shown in this figure is merely the extreme posterior end of the wider space seen in figures 8 (pl. 43) and 27 (pl. 47) which in life is full of connective tissue and lies between the posterior end of the trumpet and the posterior face of the annulus. Compare figures 2, 5, 6 (pl. 43), 11, 14 (pl. 44), 27 (pl. 47).

To summarize, we may say that the exoskeleton covering the annulus furnishes a thick-walled case about a long bent tube which opens to the exterior at the anterior end and enlarges as a two-horned pouch at its posterior end while along its entire length it communicates with the surface by curved slits leading to the zigzag suture. Essentially the annulus is a bent pocket lined by exoskeleton.

When the crayfish casts off its exoskeleton the above described shell of the annulus is thrown off as part of the entire exoskeleton. When the shell is examined from the outside, the annulus looks complete and as above described. From the inner or dorsal view the annulus of the shell is also as above described, but as it is still part of the entire shell, it does not present exactly the same face dorsally as that shown in figure 2 (pl. 43). Lying deep down between the endophragmal chambers that lodged the muscles of the bases of the fourth and fifth legs the annulus inclines downward anteriorly so that its curved ridge, or trumpet, is much foreshortened and the pits leading into the tuberosities point posteriorly and are not visible. Anteriorly the annulus is still hinged to the saddle-shaped sternum of the fourth somite while posteriorly it is continuous with the thin exoskeleton that runs from it, loosely, to the protuberant ridge across the sternum of the fifth somite.

In one specimen observed just after casting off the old shell the new shell of the annulus was translucent except for small chalky white opaque areas on the promontory and was colorless except that the two tuberosities were red.

Turning now to the living part of the annulus we find it to be a conical mass of connective tissue covered by epidermis (pl. 44, fig. 11, text-figures B and C). The connective tissue is the core of the annulus and is covered over by the epidermis which follows all the protuberances and recesses of the exoskeleton, so that the above described exoskeleton of the annulus is but the hardened outer surface of the annulus, folded in where the epidermis is folded in, and related to the connective tissue and epidermis as the crust of a loaf is to the crumb.

Removal of the annulus leaves a soft protruding surface that exudes blood which hardens into an irregular brown mass that covers the wound till the time when the animal next sheds. Then, in a few cases, it was found that upon the base whence the conical annulus was cut, a new, but very imperfect annulus had been formed. As the mass removed is part living tissue as well as exoskeleton there is some regeneration of lost living tissue; there is also the making of a new exoskeleton somewhat as would follow in the case of normal shedding without previous cutting away of the annulus (Andrews, **:06**).

The tissue that normally makes the complex exoskeleton of the annulus and has also the above slight regenerative powers, seems to be one syncytium throughout the entire annulus, hollowed out for blood vessels and lacunae and smaller cavities, full of blood and modified on the surface as an epidermis. In some cases parasites were very abundant in all these blood spaces.

The epidermal part forms everywhere a complete covering of protoplasm next to the exoskeleton with numerous nuclei in it and cell walls poorly indicated by the methods used. As shown in figures 12 and 13 (pl. 44), and 15 (pl. 45), the epidermis is continuous with the underlying network of connective tissue that has blood in its meshes. In figure 12 (pl. 44) the same continuity is shown in a preparation in which the cellular character of the epidermis was unusually pronounced. The external face of the epidermis presented various relations to the exoskeleton. Often when the epidermis was artificially drawn away from the exoskeleton, there was a finely fibrous mass, as of a coagulum, extending out from the epidermis, as indicated in figure 12 (pl. 44). In other cases the epidermis almost in contact with the exoskeleton sent out long delicate filaments that seemed to coincide with delicate tubules passing through almost all the thickness of the exoskeleton. Such tubules were seen chiefly in the walls of the tuberosities and not in the walls of the trumpet. The very much grosser tubules passing to setae are almost entirely absent from the entire annulus though a few setae were seen near the extreme outer edge as represented on the right of text-figure C. To these few hairs special strands, presumably nervous, pass through the connective-tissue network. Otherwise no nerve tissues and no gland tissues were recognized in any part of the annulus.

In some cases the sections seem to have been cut when the epidermis was active in making exoskeleton. That is, the very regular

vacuolization of the surface of the epidermis, brought about artificially in decalcification, was thought to indicate special localized states of the epidermis.

As shown in figures 12, 13 (pl. 44), and 15 (pl. 45), the connective-tissue mass of the annulus is a variable mesh of strands and plates containing scattered nuclei and continuous with the epidermis. The spaces of this net were full of blood represented in the sections by a finely granular precipitate and by a few free cells.

We thus find that the annulus is merely a conical syncytial mass full of blood and covered over by a special exoskeleton, and it seems that its usefulness as a sperm reservoir pertains to the cavity within the inert exoskeleton while the form-determining factors that make it useful, presumably reside in the living syncytium, or in other parts of the body, and not in the exoskeleton.

Having described the structure of the annulus we must next emphasize some facts in regard to its symmetry. While the annulus lies across the median line in such a way as to be balanced right and left in general form, yet there are some interesting departures from the bilateral symmetry characterizing median plates and protuberances in Crustacea. The foregoing figures show that the two tuberosities are not alike; one only has a spur passing across the median plane toward the other; the trumpet is so bent that the part on the right has no like fellow opposite on the left; the orifice is entirely upon one side and the recess though lying across the median line has one side larger than the other (pl. 43, fig. 8). Again, the zigzag suture and the curved slit passing from it to the cavity of the trumpet are not balanced right and left (pl. 43, figs. 1, 5).

In all parts of the annulus there were individual differences but the asymmetry above noted, was found in all individuals examined.

In the majority of specimens examined, the orifice was upon the right side of the animal while the tuberosity on the left sent its spur across to the right tuberosity (pl. 43, figs. 1, 5). The zigzag suture then generally passed as in figure 5, but with individual differences in length, straightness, and angle of the three successive lines, which may pass over into one another so as almost to form a sinuous, in place of a zigzag line. In some the left side of the recess may be the longer (pl. 43, fig. 8) though in others the right side may be the longer, and yet the orifice may be on the right side in each case.

But while the majority of the crayfish examined were, as we might

say, right-handed, there were also left-handed specimens. In these the symmetry of the annulus was exactly reversed (pl. 43, fig. 10; pl. 47, fig. 28). Comparing figures 5 (pl. 43) and 28 (pl. 47) we see that each is the mirror-image of the other. They also show individual differences in proportion and angle. In the left-handed annulus the orifice is on the left of the animal and the right tuberosity sends a spur across toward the left tuberosity while the zigzag and the curved slits as well as the bends of the trumpet, are all the reverse of what they are in the right-handed annulus.

Both right- and left-handed annuli were used as sperm receptacles and no difference in use was discovered.

Use of the annulus in Cambarus affinis.—As the annulus is mainly an external pocket of dense calcified exoskeleton, its use as a sperm receptacle would seem *a priori* improbable, and the important questions as to how the sperm is put into it, how it is kept there uninjured, and how it is finally got out and applied to the eggs, all demand consideration.

Proof that the annulus is indeed a physiologically necessary part of the reproductive system rests upon a number of observations and experiments.

The way in which sperm is put into the cavity of the trumpets of the annulus in *C. affinis* is, in brief, as follows. As seen in captivity, the males eagerly seize the females, from October to the early part of April, and by a complex series of adjustments, elsewhere described (Andrews, :**04**) finally fill the tube of the trumpet and the recess with sperm. During this long period females usually have the recess and the tubule of the trumpet full of sperm, while the vestibule is packed with a wax-like mass that protrudes from the orifice (pl. 47, fig. 28) and witnesses to the union with the male. But in the summer the females have little or no sperm in the annulus, at most a little in the recess.

The eggs are laid in March or early in April, and in cases under observation some weeks intervene between the reception of sperm and the laying of eggs, a period in which the female keeps away from the male and begins remarkable preparation for laying. This period in which the sperm, though carried about by the female, has not got access to the eggs is often much greater and may extend through the entire winter.

In actual isolation experiments, females kept isolated entirely for

as much as five months after sperm had been put into the annulus laid eggs that developed.

That the sperm placed in the annulus actually fertilizes the eggs, rests upon indirect evidence. In the above isolation cases, it must be that the sperm in the annulus was used to fertilize the eggs, or else that they developed parthenogenetically. But it was found that careful removal of the annulus full of sperm from females about to lay, did not prevent the normal laying of eggs, but that these eggs did not develop; while in other cases where the annulus was removed after laying the eggs, the eggs did develop, so that it seems demonstrated that the sperms preserved in the annulus are used to fertilize the eggs.

When the sperm is removed from the annulus, it soon swells and becomes disorganized in fresh water. Its preservation for so long a period is of unusual interest in these animals living in fresh water in which the sperm is transferred from male to female, not directly into the egg passages, but indirectly into an external pocket, a mere fold in the shell, kept there for weeks or months and finally brought into connection with the eggs without being destroyed by the water. This exclusion of water from the sperms embraces three periods and sets of organs from the time they leave the vas deferens till they meet the egg. In the first, sperm are transferred by the male into the annulus, in the second they are kept sealed up in the annulus, and in the third they are got out of the annulus and reach the eggs. We may refer to these as transfer, preservation, and discharge.

The details of transfer may be elsewhere described, but the chief facts are as follows. The male everts the bent nozzle-like papillae at the mouths of the vasa deferentia and through them discharges sperm into an actual tube that passes down each of the two first abdominal appendages, or stylets, and manages to keep the contact of the papilla and tube a close one by means of the special soft membrane on the second stylet of each side. Both first and second stylets right and left are locked together by a peg-and-groove contrivance. The sperm thus passes through a closed tube, as it were a temporary extension of the vas deferens formed by adding onto it the stylet tube, as far as the tip of the pointed and specialized stylet. As this tip is actually thrust into the interior of the cavity of the annulus, the sperm is put from the testes into the annulus without coming into the water.

The manipulation and introduction of sperm continues a long time

and leads to the complete packing of the recess and tube of the trumpet with sperms that fill out all the cavity, and as seen in figures 16, 17, 20 (pl. 45), and 27 (pl. 47) the mass is largely composed of actual sperms separated from one another by but a little clear matrix. That this mass of sperm flowed in under pressure seems to be indicated by the arrangement in curved lines, especially when the stream of sperms passing over the rim (that juts out to bar partly the passage from the tube into the recess) spreads out in whirls in the recess. This is shown in figure 17 (pl. 45) which represents the end of the tube and the recess cut in vertical section with the rim or bridge projecting into the passage and apparently affecting the distribution of the sperms. A greater magnification of part of this mass shows, as in figure 22 (pl. 46), that the sperms are not in actual contact with one another but are imbedded in a clear matrix and for the most part they are flattened rounded disks many of which stand on edge in this paraffin section. This is about the normal appearance of sperm in the testis and vas deferens before water has acted upon it, as elsewhere described (Andrews, **:04a**).

The preservation of the sperm in its natural shape after the transfer, depends upon the anatomy of the annulus and also upon the action of the male, both factors being necessary to keep the sperm sealed away from the water. In the anatomy of the annulus we recognized a curved trumpet with open mouth and a curved slit along its entire length. This slit, however, seems to be closed up water-tight until the eggs are laid. Its sides are very closely in contact and at the suture the cuticle seems to occlude the opening of the slit though this is difficult to be sure of, as the action of reagents and of pressure easily opens the slit and a view of an undisturbed suture is hard to obtain with high powers. It may well be that naturally the cuticle passing down into the slit on each side of its cavity, may be in such close contact with the cuticle of the opposite side as to exclude the water, though in sections, as figures 8 (pl. 43) and 14 (pl. 44), the slit is widely open.

Excluding the water from the mouth of the trumpet, there is a large mass of wax-like material that is forced in like a stopper of soft rubber into a bottle. This wax plug is furnished and inserted by the male. It is indicated in figures 14 (pl. 44) and 28 (pl. 47). It fills out the vestibule and protrudes more or less out of the orifice and at the inner end projects into the first part of the trumpet tube

where it comes into contact with the sperm. As shown in these figures this mass in not homogeneous but made up of strands or, as it were, viscid drops flowed along side by side. Where sperm and wax meet, there is more or less commingling and an appearance as if the sperm had flowed in as a less viscid mass and been followed by the wax as a more viscid mass with some intermingling of streams. In some cases the wax tended to line the walls of the cavity of the tube and to surround a central mass of sperm. Isolated small islands of wax sometimes extended in amongst the sperm and a few sperms were found cut off from the rest and lying near the orifice. Such sperms not well sealed away from the water did not have their normal form.

The way in which the male brings about this efficient closure of the cavity of the trumpet was not observed but may be inferred to be somewhat as follows. The sperm from the testis was seen in the vas deferens enveloped in a continuous tube of opaque white viscid matter secreted by the walls of the vas deferens. When the vas deferens was cut, its contraction forced out a length of this macaroni-like tube containing sperm in its central cavity and when a piece of this tube was put on a slide the sperm flowed out of its cut ends as if forced out by the shrinking of the walls of the tube. When the male transfers sperm to the annulus it is probable that both sperm and secreted tube flow down through the stylet into the annulus, but the more readily flowing sperm may pass first and fill the recess and tube of the trumpet, under combined pressure of vas deferens and shrinking secretion-tube. Later some of the pasty walls of the tube may be forced in as a viscid mass which subsequently hardens, flowing in less readily and therefore not introduced into the depths of the annulus. However, more observation is needed to determine exactly the factors actually engaged in this apparently purposeful sealing of the annulus.

The third and last protected period in the life of the sperm is that of discharge or removal from the annulus and approach to the eggs. At first it is not evident that the sperms could ever get out of the annulus and that they should be liberated at the time when eggs are near is remarkable. It is to be borne in mind that these sperms are not motile, or at the most but faintly so, and that they are injured by water.

That the sperms are actually discharged is clearly demonstrable and that this takes place when the eggs are being laid seems clear from a number of observations. The annuli of forty-five females

were studied in sections, or else in translucent preparations, and it was found that before laying, the recess and the tube of the trumpet were always full of sperm and the vestibule full of wax that projected more or less as an externally visible plug, but that after laying there was but little sperm in the tube though the recess was often still full and the vestibule was full of wax that generally still projected from the orifice.

In five females examined in June and July the plug remained though there was no sperm left except in one case in which the recess was still full. In a female examined a few hours only before laying, the trumpet tube was still full of sperm, but in fifteen females examined within twenty-four hours after the eggs had been laid, there was very little sperm in the tube and in the recess, with the exception of some cases in which the recess only was full. In fourteen of these fifteen, careful microscopic study revealed more or less sperm on the outer surface of the annulus especially along the suture as well as in the clefts leading from this suture to the cavity of the trumpet. In the exceptional case the sperm was all gone as far as study of surface views could make out, though some sperm may well have escaped notice. In most of these cases the sperm was specially aggregated on the anterior face of the promontory at the angle between the middle and anterior lines of the zigzag suture (figs. 1, 5, pl. 43), a region that may be called *the sperm angle* since it was so characteristically marked by a cluster of extruded sperms in all annuli examined not too long after the eggs had been laid. As in figure 27 (pl. 47), the sperms here may suggest the appearance of a swarm of bees and even in sections (pl. 44, fig. 14) the aggregation of sperms at this angle may be recognized. This figure shows the angle to be the meeting part of both discharging slits, the one from the anterior and the other from the middle parts of the trumpet cavity.

In figure 14 (pl. 44), which is from a female more than twenty-four hours after laying, there is present still not only the mass of sperm at the angle (pl. 47, fig. 27, shows the surface view of the same specimen) but considerable sperm within the recess and some few sperms scattering out along the posterior slit and the middle slit with a few also at the inner end of the wax plug. Yet the tube (pl. 47, fig. 27) is practically emptied and strikingly unlike the full tube shown in figure 28 (pl. 47) where the sperm mass is dark.

In another annulus examined twenty-one hours after laying, the

recess only was full of sperms and the same was true of an annulus four and a half hours after laying. In three annuli twenty-seven, sixteen, and ten minutes respectively after actual laying, there was much sperm in the recess, some in the posterior part of the tube and some spreading over the surface of the annulus.

In the annulus of a female killed in boiling water while laying (shown in figure 5, pl. 43, but with no sperm or wax indicated), there was much sperm inside the tube and recess and along the suture and spreading over the adjacent parts of the promontory as well as aggregated at the sperm angle. When first fixed, a white coagulum of sperm was seen projecting from the suture. In this case sperm from a cut up vas deferens had been placed upon the eggs to obtain views of their union and this may have got onto the annulus and vitiated the above observation, but still the main mass of sperm seen there probably came out of the annulus.

To the above evidence that sperm issues out of the slits of the annulus at the period of egg-laying, it may be objected that this was not seen in life and that the methods employed caused the sperm to ooze out. The pressure of the knife in removing the annulus sometimes causes the annulus to gape open along the suture and again after hot liquids the suture was sometimes widely opened as in figure 10 (pl. 43) which was from the female put into boiling water twenty-four hours after laying. Though an abnormal amount of gaping of the suture and some oozing out of the sperm may have been thus brought about in the methods of preparation, this did not apply to the entire phenomena, since the same general results were got when heat and pressure were avoided and various other fixatives employed.

If it be granted that there is a normal discharge of sperm from the tube through the slits to the surface of the annulus at the time of laying, the mode in which this is brought about and the way in which the sperm is tided over this critical period to reach the egg without injury from the water, are questions upon which some light is shed by the following observations and experiments.

The habits of the female at the period of laying, as elsewhere, described (Andrews, : 04 and : 06a), are briefly stated as follows. She seeks a protected locality and for some days assiduously cleans all the ventral side of the abdomen and the region about the annulus. Then standing high up upon her legs she allows the secretion of the "cement glands" of the ventral side of the abdomen to run down over the

pleopods or swimmerets, where it swells up and forms an almost invisible mucus-like mass hanging down from the pleopods. Very soon the female bends the abdomen forward under the thorax and deliberately lies down upon her back. The abdomen with its caudal fan widely expanded, is stretched so far forward over the thorax as to cover the bases of all the thoracic legs. The mucus-like secretion now adheres to the thorax as well as to the abdomen and the space between the ventral sides of the thorax and abdomen is filled up by this clear secretion. On the sides, the extensions of the abdominal pleura nearly close in this space so that a chamber full of mucus is formed. As the oviducts open on the bases of the third pair of thoracic legs (text-figure A), the eggs may come out into this chamber, a chamber into which the sperm might also issue and a chamber containing all the pleopods to which, as is well known, the eggs are affixed soon after being laid.

On several occasions the actual issue of eggs from the two oviducts was seen. They flowed out in two streams as semiliquid masses, each egg distorted by pressure, and seemed forced out by rhythmic contractions, as if of the oviduct or the ovary. The female lay in such a position that the ventral surface of the thorax was inclined posteriorly and the streams of eggs were led by gravity downward and posteriorly into the above chamber. The concave surface of the sternal plates of the fourth thoracic somite (text-figure A), tended to concentrate the eggs toward the annulus so that they flowed over and close to the annulus before passing posteriorly into the chamber as into the hollow of a hand. Many eggs imbedded in the mucus or glaire were seen to flow slowly over the annulus.

If, as above maintained the sperm comes out of the suture of the annulus at the time of laying and spreads out over the surface of the annulus it must come into the mucous secretion. But attempts to find it in the mucus and upon the eggs failed. The mucus, however, was not coagulated by 85 degrees water followed by Perenyi's liquid and was often easily washed off in preparations, but yet in some preparations a residue of glaire was found on the annulus. Thus in one case less than twenty-four hours after laying, the annulus was covered by a thick layer of glaire and when fixed in cold Worcester's liquid and sectioned after carmine stain there were remnants of a coagulum over the annulus and some sperms in this mass.

As these sperms were expanded and no longer in the form they have

in the vas deferens, it might be thought the period of discharge was not also a continuation of their protection from water but that they were now acted upon by water to some extent before they meet the eggs. However, it seems that the mucous secretion probably does protect the sperms from the action of water even after they are discharged from the annulus, for another annulus fixed in Flemming's solution sixteen minutes after laying shows (pl. 45, fig. 19) the sperms in the unchanged form crowded out of the suture and spread over the annulus. Only a small part of the promontory is drawn, with the posterior line of the zigzag on the right covered by a dense mass of sperms and more and more sparsely scattered sperms over the surface toward the left. Some of the sperms show the characteristic Y appearance within the bowl or vesicle and they are in the normal shape as given by osmic preparations. The three large dark masses represented, were secretion spherules such as crowd the mucous mass and may be obtained by cutting open the "cement glands" of the pleopods. These sperm were all imbedded in a grayish coagulum, the fixed glaire or mucus, probably.

It thus seems that the secretions of the female with her habits of laying, produce an environment for the sperms as they are discharged that protects them from the water while at the same time they are spread out in the path taken by the eggs on their way to be fastened to the pleopods. A secretion of the female guards the sperm in this last phase as a secretion of the male protected them before.

The view that the secretion of the cement glands is a means to keep the sperms unchanged till they meet the eggs does not exclude the generally accepted view that it is a means of fastening the eggs to the pleopods. An attempt this season to decide this latter question with reference to Williamson's (: 04) claimed use of the pleopod hairs in crabs has led to grave doubt as to the extension of this view to the crayfish; however, the problem of exactly how the eggs are attached to the pleopods in the crayfish remains unsettled (Andrews, : 06b). The baffling question as to how the sperms and eggs unite, seems involved in the making of the outer case by which the egg is fastened to the pleopod and remains for the present undecided.

Before considering the means by which the sperms are discharged from the annulus, we will show that though a great many sperms remain in the annulus, enough are set free to fertilize all the eggs. The number of eggs laid at one period is about 200 in small and 400 to

500 in larger females and as many as 631 in a very large female. After laying, the number of sperm left behind in and upon the annulus was roughly estimated from surface views and sections to be some 10,000, most of which were in the recess. All these were thought to be of no use, for when an annulus with its large remnant of sperm was removed from a female about twenty-four hours after the eggs were laid the eggs developed and hatched in fifty-one days just as did those of a control in the same aquarium.

Before laying, the amount of sperm within the annulus is very much greater and some estimate of the number of sperms stored there was obtained by the following means. An annulus was dried with filter paper and dissected under the microscope to remove the sperm plug with adherent sperm. In a drop of strong potassic nitrate solution the sperms oozed out and dispersed through the liquid so that their number could be roughly estimated and it was found to be about 35,000. Again, such a plug was put into a minute drop of water on a circular cover 7 mm. in diameter till most of the sperm had dispersed, then transferred to a second cover and washed about to remove the remaining sperm. Rubbing the two covers together distributed the sperms uniformly and they were then dried and stained with dahlia as smear preparations. The sperms were then counted over one half of each cover and the number estimated for one female was 14,814, for another 19,372 and for another case when four covers were used 25,636 were estimated. The last was probably less inaccurate than the other two. In this method, the sperm from the recess and from the posterior end of the trumpet tube was not obtained and the above numbers must be too small. By counting several areas in each of twenty successive sections through the annulus of a female killed in December when the annulus was already full of sperm, a much larger estimate, 50,000 to 60,000 was obtained.

We conclude that, while some thousands of sperms may remain within the annulus after the eggs are laid, many more thousands are discharged when the few hundreds of eggs are flowing by and thus there is numerically ample supply for the fertilization of all the eggs. As a matter of fact, very few of the eggs, even in confined specimens failed to develop unless from reasons obviously not connected with the amount of sperm. Unless parthenogenesis occurs we must conclude that all the eggs are necessarily fertilized as a result of the above described discharge of sperm from the annulus.

In this connection, it may be pointed out that there is ample provision for filling the annulus. In captivity, at least, the males are long active in filling the annuli of as many females as they may find and they have abundant sperm for this purpose. In filling the annulus there seemed to be no loss of sperm and on the other hand the number of sperm in one millimeter of the middle part of the vas deferens of a male in March was calculated to be 16,452, by the above cover-glass method. As the entire length of each vas deferens was 60 mm., there were about 2,000,000 sperms available in the vasa deferentia at one time. The contents of three or four millimeters length of one vas deferens would fill the annulus of one female and the entire amount would fill from 30 to 40 annuli.

Coming finally to the question of how it is that sufficient sperm is discharged from the annulus at just the right time to meet the eggs, there is evidence that a muscular act of the female associated with the secretion of glaire and the discharge of eggs is a prime factor. When the female remained upon her back in the period of egg-laying it was noticed that the fifth pair of legs was held stiff in a peculiar attitude with the tips bent backward as elsewhere figured (Andrews, : 04). The bases of these legs were concealed by the abdomen during laying but in one case where the abdomen was forcibly raised it was found that the peculiar transverse ridge on the sternum of the fifth thoracic somite (text-figure A), was firmly pressed against the posterior face of the annulus as late as sixteen minutes after laying. And a horizontal section of this annulus (pl. 45, fig. 19) shows the sperm spreading from the suture. By forcibly moving the legs it is found that the movable fifth somite can be forced to press its sternal ridge against the annulus. It is probable that the observed attitude of those legs is accompanied by such pressure of the sternal ridge against the annulus as was actually observed in the above case.

To determine if pressure on the posterior edge of the annulus would cause it to discharge, three specimens that had not yet laid, were subjected to strong pressure against the posterior face of the annulus *in situ*, either by direct pressing with forceps or scalpel, or by pressing the fifth sternum against the annulus. In both ways and in all three specimens, there was a visible oozing of liquid from the suture of the annulus, which had previously been dried with filter paper. As the sperm, if discharged, was readily floated away and lost in preparation and as no success was obtained in attempting to see

it in fresh specimens, white of hen's egg was spread over the annulus and then fixed to hold the sperm in place. In one whole mount of such an annulus the stained sperms were seen spread out in a layer from the suture over the promontory and also over the left tuberosity, though this was a left-handed annulus. In the other specimen was found the condition seen in figure 18 (pl. 45). The sperm was fixed in large clots of the egg albumen spreading out from the "*sperm angle*" across the transverse depression and along the first line of the zigzag and also spreading out from the second and the posterior lines of the zigzag.

This is a fine demonstration of the discharge of sperm from an annulus subjected to pressure and it differs from the appearances seen in a normal annulus just after laying only in the larger amount of sperm actually seen. But this greater amount is to be explained in part by the egg albumen holding it there and in part by the fact that in normal laying the current of eggs and surrounding glaire would tend to carry off the sperm, and again, the method of preparation would remove some sperm. We may suppose that the normal discharge of sperm would present much the same view as that seen in figure 18 (pl. 45).

Since artificial pressure against the annulus forces out sperm much as in normal discharges and as the female appears to contract the muscles of the fifth somite in such a way as to produce a like pressure, we may conclude that it is by this muscular contraction that the female brings about the discharge of the sperm and the ultimate fertilization of her eggs.

The sperms spreading over the promontory and adjacent areas of the annulus are not expanded (pl. 45, fig. 19), and probably have little or no power of locomotion. Their extension over the surface may be due to some physical phenomenon connected with the fact that they are imbedded in a liquid matrix that might well spread by surface tension.

The actual emergence of the sperm from the annulus seems to be the direct result of mechanical pressure. In several experiments in which very strong pressure was exerted, the wax plug was noticeably protruded as if pressure squeezed the contents of the trumpet. In normal laying, the plug remains in place but there may be enough compression of the trumpet to squeeze out the sperm through the surface. The opening of the suture may well be caused by the same pressure

since the anatomy of the annulus favors the idea that a compressing force exerted from behind forwards might make the zigzag suture (pl. 43, fig. 1, and text-figure B) spring open, especially at its angles.

There still remains the possibility that the glaire secreted by the female may play some part in discharging the sperm from the annulus; possibly it may penetrate into the orifice and cause an expansion of the contents of the trumpet; but the mechanical pressure in actual experiments was the only factor necessary, unless the egg albumen played a part.

The recess commonly remains full after the tube is emptied though it may be emptied at the same time (pl. 43, fig. 10). This behavior of the recess might be explained upon the hypothesis that the penetration of glaire was necessary to discharge it, for it was noticeable that in staining annuli the recess remained very long unstained, and again when finally stained, was very slowly decolorized so that the accessibility of the contents of the recess to liquids from without is much less than that of the contents of the trumpet tube and thus the recess would long remain unaffected by glaire. On the other hand mechanical pressure alone may conceivably sometimes discharge the recess and the common failure to discharge is what we would expect unless the pressure were very great. For from figure 14 (pl. 44) and the series of sections (pl. 43, fig. 8; pl. 45, fig. 16), it is evident that the recess is too firmly embedded in the thick exoskeleton to be readily compressed and, moreover, its connection with the exterior is so indirect and restricted that discharge would seem more difficult than from the trumpet tube.

In conclusion, we seem justified in supposing that mechanical pressure furnished by the female is the cause of the cracking open of the annulus and of the squeezing out of sperm which then spreads by surface tension. However, the possibility that the secreted glaire may take part in the emergence of the sperm or even in the opening of the suture, is not absolutely excluded.

Structure in Cambarus virilis.— To determine if the use and structure of the annulus described in *C. affinis* was peculiar to this species or common to all the genus, a few other species were selected at random and studied sufficiently to indicate that the latter alternative is the probable one. In *Cambarus virilis* brought here from Chicago markets, several cases of pairing were observed in October and November and the habits of the male seem to be essentially the same as in *C. affinis* (Andrews, : 04).

The sperm placed by the male in the annulus, filled all the posterior part of the trumpet tube as shown in figure 21 (pl. 46). When the annulus was dried and broken open, the contents of the tube came out as a flat, curved plate of wax-like substance which in water swelled up and allowed sperm to spread out from its tip and from any broken part. The posterior part of this cast of the cavity of the annulus presented a slight enlargement to fit the terminal enlargement of the tube shown in figure 21 (pl. 46).

The position of the annulus is that found in *C. affinis* (text-figure A), and it is also hinged to the concave sternal plate anterior to it so that its posterior edge may be pushed dorsally to displace the soft tissues above it but cannot be pulled downward below the horizontal position it assumes when left to itself. The annulus differs from that of *C. affinis* (pl. 43, fig. 1) in being larger and truly annular in appearance as seen in figure 29 (pl. 47). The large central depressed area is surrounded by a high rounded rim, or ring. The posterior half of the rim passes gradually into the depressed area, anteriorly. But the anterior half of the rim stands up away from the depressed area as two bolsters or cushions, one right, one left of a median groove. These cushions may be indented by a needle point and in life they are sometimes red while the posterior parts of the annulus are greenish or bluish, but often the entire organ is creamy white. Only the posterior half of the annulus is well calcified and when cleared in oil of cloves this part remains opaque white while the anterior half looks like translucent chitin.

The zigzag suture coming from the posterior face over the rim passes, like a stream at the bottom of a valley, forward and downward across the depressed area to disappear under the anterior cushion on the right. In its course the zigzag presents six successive component lines. Thus, leaving the median plane, it passes a short distance to the right, then a longer distance to the left, then a shorter distance to the right, nearly parallel to its second course, then a long distance to the right and finally forward and somewhat to the left under the cushion. Of the five angles along its course, the second and third from the posterior end are marked by long extensions of the line beyond the point of meeting the next line of the zigzag. Most of the length of this line is a mere closed groove, but the anterior two stretches are wide open clefts becoming anteriorly an open orifice under the cushion.

The floor of the depressed area juts out right and left in hills and

ridges bounded by the parts of the zigzag. Two ridges are especially prominent; a long one on the left running along the second and third parts of the zigzag, counting from the anterior end, a short wide ridge on the right opposite to the left ridge across the suture valley. In dried specimens and often in life, these two ridges are often more pronounced than in figure 29 (pl. 47). They then suggest the idea that they may be homologous with the two tuberosities of *C. affinis*, the one on the right passing across the median line somewhat as does the spur in figure 1 (pl. 43). In this hypothesis, the orifice of figures 1 and 5 would represent the third angle of the zigzag of figure 29 (pl. 47), leaving posterior to this angle a three-limbed zigzag that is very similar in both species; thus a depression of the tuberosities of figure 1 and extension of the zigzag and an elevation of the anterior edge of the annulus to form two cushions would form an annulus like that of figure 29 (pl. 47).

Removing the annulus and looking at its exoskeleton from the dorsal side (pl. 47, fig. 31), we see a long and much bent ridge corresponding to the zigzag suture in its course. This ridge presents four successive semicircular sweeps to right and left alternately, of which the most posterior is lost to sight in the deep depression representing the elevated posterior rim seen in figure 29 (pl. 47). The anterior part of the ridge stands up very high from the rest and from it run off buttresses right and left. These represent the obverse of the most depressed anterior part of the central areas seen in the ventral view (pl. 47, fig. 29). The anterior median elevation in figure 31 (pl. 47) is the obverse of the median anterior groove between the cushions. The elevation of the anterior part of the ridge is indicated in figure 35 (pl. 47) where the two cushions and the median groove forming the anterior face of the annulus are represented above, while the downhanging tube is the elevated ridge passing off on the left into the depressed central area seen in figure 29 (pl. 47), which is the same as the lateral buttress seen on the left, next the ridge, in figure 31 (pl. 47).

A posterior view of the annulus (pl. 47, fig. 32) shows that its face here is very steep and high and that the median part of the zigzag suture extends down over the posterior rim a short distance. This also presents the annulus as a ring with an anterior notch.

Upon decalcifying and clearing the exoskeleton of the annulus it was found that the dorsal ridge was really a long bent tube (pl. 46, fig. 23) which from this dorsal view presented anteriorly a wide open

vestibule extending over to the right as a flattened pocket that opened downward in the anterior part of the depressed area somewhat under the edge of the cushion. In this specimen it opened under the cushion on the left while in the specimen shown in 29 and 31 (pl. 47) it was on the right, these being two cases of right- and left-handed symmetry. Posterior to this vestibule, which is empty (pl. 46, fig. 23), followed a semicircle of tube full of flaky material which was the wax-like substance that plugged up the cavity as far back as to the median line at the end of the second semicircle. The two following semicircles, to the right and then to the left, were full of sperm which is represented by dotted areas in figure 23. The sperm tube ends in a slight enlargement of the median line and just posterior to this is a small and apparently isolated pocket of sperm. The exoskeleton walls of this long, much bent trumpet are seen to be rather thick but relatively much less so than in *C. affinis* (pl. 43, fig. 5).

The relationship of the cavity of the trumpet and the zigzag suture was made out in such ventral views of translucent annuli as that shown in figure 21 (pl. 46), which is a specimen having the same symmetry as the one in figures 29 and 31 (pl. 47). Here certain areas were opaque, that is, all the posterior half of the annulus to some extent and the posterior faces of the cushions, where seen through their depths. Showing through the translucent floor of the central depressed area, the thick walls of the trumpet tube are seen enveloping its cavity and anteriorly passing over into continuity with the exoskeleton of the floor of the depressed area. On the translucent surface of the annulus runs the zigzag suture, coinciding in its sharp turns with the smooth curves of the overlying trumpet tube. From the posterior end forward, we see a blunt median ending of the tube above the median line of the suture, an arc to the left alongside of the second line of the suture, an arc to the right and anteriorly alongside of the third line of the suture, an arc to the right alongside of the fourth line, a transverse and posterior arc along the fifth line, and an arc on the right of the sixth line. The two last arcs are but the walls of the vestibule, or flaring flattened mouth of the trumpet, where it opens upward in the figure into the most depressed part of the ventral surface of the annulus. The two anterior lines are but parts of the rim of the vestibule. The four other lines are the tightly closed mouths of curved clefts leading to the arcs of the tube and thus putting the whole length of the tube into morphological communication with the exterior.

In this species, the thick cuticle over the exoskeleton is often red brown and not only makes the zigzag plain but extending inward to line the cavity of the annulus, enables one readily to trace the clefts from the surface suture to the cavity of the trumpet. Thus in figure 33 (pl. 47), which is the enlarged posterior part of a preparation like figure 21 (pl. 46), the three dark lines represent the first, second, and part of the third lines of the suture, and from these the closed clefts could be followed by focussing through the exoskeleton as far as the dotted line. This represents the inner end of the curved planes, or closed clefts, leading first from the median suture to the right and anteriorly to the last part of the trumpet cavity and next to the left and anteriorly to the semicircle of trumpet cavity shown on the left. These two planes crossing, there is a complex puckering and an extension of the suture where the median and next suture lines meet. The cavity here represented empty was in reality full of sperm which extended forward far into the next arc as seen in figure 21 (pl. 46) and was then succeeded by wax that filled all the rest of the tube and the vestibule nearly to the last line.

The above illustrations suggest that the trumpet is a long flat pocket open anteriorly and closed along the rest of its length; a pocket not straight but folded right and left and with its mouth drawn smaller than its bottom and thrown into sharp zigzag lines.

Owing to the absence of such hard tuberosities as those of *C. affinis* and to the small amount of calcification, the annulus of *C. virilis* was readily cut into serial sections and the general structure found to be the same as in *C. affinis*. The exoskeleton that forms the walls of the trumpet is but an inward continuation of the exoskeleton of the rest of the annulus and the outer cuticle over the crayfish runs in at the vestibule as well as along the entire suture to line the entire cavity of the trumpet which is thus morphologically but a pocket in the exoskeleton. This exoskeleton pocket, however, lies upon a basis of epidermis and connective tissue that is like that in *C. affinis* and is the infolded living material that made the exoskeleton.

At first *C. virilis* seemed to lack the peculiar part of the annulus called the 'recess' in *C. affinis* but closer study showed a small cavity comparable to the recess. In figures 21, 23 (pl. 46), and 33 (pl. 47) is seen a small curved sac posterior to the posterior end of the trumpet and somewhat to one side. This corresponds to the large heart-shaped recess of *C. affinis* seen in figures 27 (pl. 47) and 10 (pl. 43).

In *C. virilis* the recess is at most only half a heart and as the tip of the trumpet tube is enlarged and wide, the recess seems doubly insignificant and it is easily overlooked especially since it is full of sperm as is likewise the tube. Dorsally, however, it extends to some depth and in a transverse section (pl. 47, fig. 30) across the tip of the tube it is represented by a rather large pouch running up on one side of the tip of the tube. On the other side there is also a faint sac and the two together if greatly enlarged where discharging, might form such a recess as shown for *C. affinis* in figure 8 (pl. 43). The apparent nature of the recess as a puckering-in of the exoskeleton to make a pocket where the posterior end of the tube opens by a narrow slit to the external suture, is clearly indicated in *C. virilis* and this same interpretation may well be extended to *C. affinis*.

The use of the annulus in this species is sufficiently evident from the fact that all the twenty-one females examined in autumn and winter had the annulus full of sperm. No observations were made upon the mode of discharge, as the specimens all died in captivity before laying. In only one case was sperm seen on the external surface, along the median suture.

From the great length and size of the trumpet, there seems opportunity for greater storage of sperm than in *C. affinis*, but part of this is not used, since the wax is run in nearly as far back morphologically as it is in the former species leaving about the same morphological extent of tube for sperm. Comparing figures 21 and 23 (pl. 46) with figures 5 (pl. 43) and 28 (pl. 47) we find that the sperm runs forward only about one arc farther in the long tube than in the short tube, the greater length gained by *C. virilis* being used largely to pack in more wax anteriorly. The wax often projected slightly as a plug at the posterior end of the fifth line when it ran along a gaping suture, and in other cases the plug projected from the angle where the fifth and sixth lines joined. In all cases the plug being deep down in the depressed area under the cushion, was not conspicuous as it was in *C. affinis*.

As already indicated, the phenomenon of right and left symmetry was seen here as in *C. affinis*. Of fifteen specimens only one had the orifice upon the right of the animal, but of six others, three opened upon the right; thus the great majority of the twenty-one studied opened upon the left.

Comparing a right- with a left-handed annulus (pl. 46, figs. 23 and

21), we see that they have the same curves when looked at one from a ventral, the other from the dorsal side; in other words, they are mirror images of each another. This reversal of symmetry may extend even to the recess; thus in figures 21 (pl. 46) and 33 (pl. 47) the recess is on the animal's right and the orifice of these annuli on the animal's left, but in figure 23 (pl. 46) which is the rare form of symmetry, the recess though nearly median was more on the animal's left in this case where the orifice was on the animal's right. However, as in *C. affinis* the position of the recess is probably too variable to be safely brought into consideration of right- and left-handedness. There are also marked individual differences in all parts of the annulus, in the size and position of the various parts of the trumpet, in the angles and lengths of the lines of the zigzag, in the amount of depression of the ventral surface, and in the amount of elevation of the cushions.

In comparing the right- and left-handedness of *C. affinis* and *C. virilis* it is to be noted that most of the former had the orifice of the trumpet on the animal's right side while most of the latter had it on the animal's left side. Should an examination of a very large number of individuals show that one species is predominatingly right- and the other left-handed, it would be interesting to ascertain what relation this bears to the assumed homology suggested above between the posterior three lines of the suture of one species and those of the other. That is to say, if the posterior part of the zigzag in each species be fixed and the great length of the suture in *C. virilis* be regarded as obtained by an anterior addition of three lines to the three alone present in *C. affinis*, then the position of the third angle in *C. virilis* would be the homologue of the orifice in *C. affinis*. The two tuberosities in the latter species would be imagined as reduced to the two ridges right and left of this third angle in *C. virilis*. As this third angle in *C. virilis* is on the right (pl. 46, fig. 21; pl. 47, fig. 29) when the orifice is on the left of the animal and on the left when the orifice is on the right (fig. 23, pl. 46, s udied with fig. 31, pl. 47), in other words, since the third angle is on the side opposite to the orifice, it follows that if the angle be homologous with the orifice of *C. affinis* then the orifice of *C. virilis* is a new one on the opposite side. Thus the prevalence of left-handed orifices in *C. virilis* would be deduced from the prevalence of right-handed orifices in *C. affinis* and both species would agree in having right-handed annuli as the prevalent form so far as the fundamental posterior parts were concerned.

On these assumptions a right-handed *C. virilis* would be fundamentally like a left-handed *C. affinis* and in both species these seem to be the rarer forms.

Structure in Cambarus clarkii.— Some thirty-one females of *C. clarkii* from New Orleans when studied in November had only small eggs in the ovaries and no sperm in the annuli. In the males the testes were small but the vasa deferentia contained apparently mature sperm. No pairing habits were seen, but one female kept with males laid eggs in March and these developed and hatched.

The annulus in this species has the usual position but it is markedly small and inconspicuous in comparison with the annuli of the above two species. The median transverse ridge upon the fifth thoracic sternum is also small. The annulus is movable dorsally upon its anterior hinge and by moving the fifth legs one may push the fifth sternal ridge against the posterior face of the annulus which enables one to suppose the annulus may be discharged by pressure as was thought to be the case in *C. affinis*.

The annulus is whitish or light red and may have a blue area right and left upon its anterior face; it is thus noticeably paler than the adjacent parts which have the vivid red color of the under side of this highly colored species.

The form of the annulus (pl. 47, fig. 34) is that of a truncated hill very slightly dished on top so it seems to depart markedly from the preceding forms in having no central depressed area. It is also characteristically smooth, simple, and free from protuberances, while its plain single suture is all in sight. The central plateau is bounded by a steep slope leading down gradually to the general level of the adjacent sternal surface so that the exact delimitations of the transversely and sharply ellipitical annulus are not at all well marked. The posterior view (pl. 48, fig. 37) well shows the truncated character and the slightly greater elevation of the median posterior border. The anterior face (pl. 48, fig. 38) shows a deep median groove from which the sinuous suture passes back.

The suture passes from the median line to the right or the left, in one angular semicircle and returns, anteriorly, nearly to the median line to break through the anterior border of the plateau into the wide median groove on the anterior face of the annulus. This anterior groove seems an exaggerated representative of the corresponding part of *C. affinis* (pl. 43, fig. 1).

In some specimens the plateau is nearly smooth as in figure 34 (pl. 47), in others the suture is at the bottom of a somewhat pronounced valley and the sides of this valley often stand up as ridges parallel to the suture. Anteriorly, especially, these ridges are very pronounced and tend to simulate the tuberosities of *C. affinis* though they are never as prominent.

Removing the exoskeleton of the annulus and regarding its dorsal surface (pl. 48, fig. 36), we find it the obverse of figure 34 (pl. 47), that is, from its edges there is a steep slope down into a deep pit with a flat bottom. Across this runs, deep down, a small simple trumpet-ridge ending posteriorly in a bulb and anteriorly continuous with the deeper, ventral part of the groove of the anterior face (pl. 48, figs. 36, 37, 38). Like almost all of the annulus, the dorsal ridge or trumpet is highly calcified, floating in alcoholic picrosulphuric with evolution of gas, and it looks like a piece of glazed china.

The surface of the groove on the anterior face of the annulus is glazed and yellowish. The entire organ seems to have little flexibility and the introduction of sperm into it would seem to present difficulties.

Decalcified and cleared, a ventral view of the annulus (pl. 46, fig. 24) shows its great simplicity. Seen through the exoskeleton of the top of the plateau the trumpet ridge is a thick-walled tube with three bends, right and left alternately. This tube follows the suture very closely and its cavity is nowhere far removed from the suture. Moreover, the suture like the tube shows but a simple and continuous change in course with little of the character of successive straight lines seen in *C. affinis* and *C. virilis*.

Fig. D.

The cavity of the trumpet connects by very short clefts with the suture and in paraffin sections these gape open as shown in text-figure D which represents a cross section of the posterior part of the annulus.

In nature the suture is closed except for a small chink anteriorly near the median line (pl. 46, fig. 24), and this represents the orifice and leads into a very shallow and simple vestibule or anterior part of the trumpet tube. The tube does not therefore open anteriorly into

the groove on the anterior face of the annulus, as might be supposed (pl. 47, fig. 34), but the sharp cleft in the anterior rim of the plateau puts the anterior groove into direct communication with the suture (pl. 48, fig. 38), which thus seems to run forward into that groove (pl. 47, fig. 34).

A general view of the exceedingly simple cavity of this annulus is given in figure 39 (pl. 48) which represents a thick longitudinal section cleared in oil of cloves and seen from the left side, anterior being to the right and ventral above. On the right is seen the steep anterior face, on the left the steeper posterior face, and above, the top of the plateau whence projects downward the trumpet and its cavity opening to the surface by widely opened clefts. On the right in the background is the far, or right, side of the groove of the anterior face (pl. 47, fig. 34; pl. 48, fig. 38); the heavy line represents the bottom of the groove. This bottom line rises over a 'divide,' which is the top of the slope leading up the outer face, and it then falls down through the narrow cleft in the anterior rim of the plateau to the bottom of the suture plane or mouth of the orifice. Thence to the left in figure 39 (pl. 48) the dark line is the bottom of the cavity of the trumpet. This tube cavity is but a slight enlargement of the opened suture plane leading to the surface. Toward the right of figure 39 (pl. 48) it is seen in cross section as it comes somewhat toward the observer and then it passes far away to the right of the animal (pl. 46, fig. 24), to return toward the observer and be cut across again in this section. The terminal part of the cavity on the left of the figure is the posterior median part of figure 24 and, lying near the plane of the section, is represented as a light area, enlarged below and opening to the surface by an open cleft.

The above views make self evident the interpretation of the exoskeleton of the annulus as an elevated mass pitted in as a crooked longitudinal pocket whose mouth is open all along its length in some preparations, but in Nature closed except for a short distance anteriorly.

While such views as figure 24 (pl. 46) and figure 39 (pl. 48) seem to show that the annulus is more simple in possessing no recess, yet some cross sections, text-figure D, show a small posterior cavity near the tip of the tube and apparently isolated from the median suture. This is, however, but the tip of the trumpet tube itself and not a side pocket or recess. The appearance of an isolated recess is due to the fact

shown in figure 39 (pl. 48), that is, that the tube cavity ends bluntly some distance anterior to the ending of the suture on the surface while the plane or slit connecting suture and cavity of tube ends in a slanting wrinkled line leading from the posterior end of the surface suture inward and forward some distance to meet the cavity of the tube as shown in figure 39 (pl. 48). A very thin section, as in text-figure D, may thus cut across the tip of the trumpet tube surrounded by solid exoskeleton and also cut the outer part of the posterior ending of the suture slit. Sperm, if it were forced along the tube, would readily pass out of the suture, when opened, and find no recess or side pockets to lodge in.

Thus this annulus is simple both in having no specialized vestibule and in having no recess.

Owing to the great simplicity of this annulus it is possible to pull away the exoskeleton from the underlying soft tissues and to obtain (pl. 48, fig. 40), as it were, the die upon which the exoskeleton was made. Seen from the ventral side the living part of the annulus thus laid bare is a projecting mass of connective tissue covered by epidermis and with a curved longitudinal groove along it. The elevated mass projects anteriorly on each side and posteriorly it somewhat overhangs the epidermis of the sternal surface posterior to the annulus. The bluntly ending posterior part of the groove is on the median line and more anteriorly the groove sweeps in a semicircle to one side, finally to pass over a ridge down into the deep depression upon the anterior face of the annulus. The external suture of the exoskeleton (pl. 47, fig. 34) thus indicates the axis of the groove of epidermis shown in figure 40 (pl. 48). The posterior boundary of the groove is a narrow transverse elevated rim which is the tissue that fits into the space shown in figure 39 (pl. 48) between the exoskeleton of the posterior face of the annulus and the exoskeleton of the trumpet.

While the essentially living part of the exoskeleton is thus an elevation bearing a bent groove, the exoskeleton that fits over this tissue annulus is so thick that it nearly fills the groove solidly and leaves but a small cavity connecting with the exterior by a fine slit. Thus the wide flaring epidermis groove (pl. 48, fig. 40) is occupied by a thick-walled pocket (pl. 46, fig. 24) and the wide external opening in the epidermis is reduced to a suture open for a short distance only, anteriorly, as the orifice into the exoskeletal tube.

The microscopic structure of the tissue annulus (pl. 48, fig. 40) is

like that of *C. affinis*. A layer of epidermal cells everywhere covers this mass and underlies the exoskeleton. The bulk of the mass is a loose areolated connective tissue with its spaces full of blood and it is interspersed with large lacunae. Above the epidermal groove of the annulus runs the sternal artery and above that the nerve cord, just as in *C. affinis* (text-figures B and C).

Though so simple, the annulus of *C. clarkii* is not bilaterally symmetrical. While the suture begins and ends on the middle line, it sweeps off to one side (pl. 47, fig. 34) and the trumpet (pl. 46, fig. 24; pl. 48, fig. 36) is differently disposed on the right and the left of the animal since the formative epidermal groove (pl. 48, fig. 40) has much of its course upon only one side of the median plane. And, as in the previous two species, the open part of the suture, that is the orifice, is slightly to one side of the median plane. Of twenty-nine specimens, sixteen had the large loop of the suture passing to the animal's left and thirteen had it to the right. In the former (pl. 47, fig. 34) the orifice was somewhat on the animal's right and in the latter somewhat on the animal's left (pl. 46, fig. 24). While the position of the orifice is not far from the median plane and its determination often uncertain, there are undoubtedly right- and left-handed specimens in this species, and, so far as observed, a slight majority had the large bend of the trumpet on the left and the orifice on the right so that they might be called right-handed in the same sense as the majority of *C. affinis*.

Structure in Cambarus bartoni.—Specimens from Baltimore Co., Md., studied in April and May were from 60 to 73 mm. long in four cases and smaller in the others. Some had no sperm in the annulus and others had some sperms in the recess and tip of the tube only (pl. 46, fig. 25). The breeding season is much earlier and this retention of sperm in the recess is the same phenomenon met with in *C. affinis*.

In shape, the annulus (pl. 48, fig. 41) is markedly rhomboidal in outline, well elevated and truncated. It has a depressed area posterior to the center. Its anterior face (pl. 48, fig. 43) is a long slope reaching to the center, while its posterior face (pl. 48, fig. 44) is steep and high. A marked but narrow median groove runs up the anterior face and then bends to one side on entering the depressed area. This area is bounded by a high rounded rim posteriorly and on the sides as well as anteriorly, but on the median line anteriorly the rim is interrupted by the above groove (pl. 48, fig. 43).

The suture is short and curved, not readily resolvable into a zigzag of lines. Coming across the posterior rim of the depressed area as a line passing away from the median plane to one side, it then suddenly bends to the opposite side across the median plane and then down the depressed area along its posterior boundary far to one side to disappear under the lateral elevated rim of the depressed area.

The floor of the depressed area is chiefly a transverse ridge or tongue that passes across the median plane parallel to the suture and likewise disappears under the elevated lateral rim of figure 41 (pl. 48). This transverse tongue goes from the posterior rim of the annulus on one side far over to the opposite side of the annulus. It is marked off posteriorly by the transverse part of the suture and anteriorly by a wider groove. The deepest part of the depressed area is far to one side.

The color of the annulus made it noticeable. It was often reddish yellow and posteriorly greenish while the central tongue was white, but there were many individual differences.

The annulus was well calcified except that the bottom of the median anterior groove and also the groove along the anterior edge of the transverse tongue were thin and translucent. On each side of the anterior face far from the median groove there was also a thin and partly calcified area.

The dorsal aspect of the exoskeleton (pl. 48, fig. 42) shows the trumpet tube passing very far to one side and lying near the posterior edge of the annulus in correspondence with the like position of the external suture (pl. 48, fig. 41). Though this figure fails in showing it, the anterior face of the annulus rises up above the general level so as to form a wide angle with the rest of the annulus and being about half the entire length of the annulus the appearance might be compared to a small 'wall pocket' in which the posterior part of the annulus juts out from the anterior half as a pocket holding the trumpet tube in it.

The trumpet tube, followed from its posterior end where it is nearly median, turns abruptly to one side and runs transversely. It is this part only that is at all conspicuous as it stands up above the adjacent parts so that it shows from the posterior view (pl. 48, fig. 44) against the background furnished by the low-hanging anterior face of the annulus. Then, far from the median plane, the tube becoming more and more depressed, turns back as a second bend and sinking into the general level of the exoskeleton, approaches the median line again.

The remarkably transverse position of the tube is appreciated when a decalcified cleared specimen is looked at from the ventral side (pl. 46, fig. 26). Here the suture is indicated by the two dark lines. The short one passes from the middle of the posterior edge of the annulus to the right and soon meets the long second line sweeping forward and to the left. The other dark line on the left indicates the edge of the abrupt overhanging left rim of the central depression. This edge running as the left edge of the groove of the anterior face and coming into the depressed area, sweeps to the left, and then returns towards the median plane to cross the suture line. The short chink formed between these two lines is the right end of the transversely placed orifice of the annulus. The rest of the orifice is still farther to the left under the overhanging rim that conceals the left end of the tube. The tube, or cavity, of the annulus is shown as a narrow clear space passing from the above orifice far over to the right of the annulus and then posteriorly to end as a marked enlargement or bulb. This terminal bulb of the tube is on the right of the median line.

Just posterior to this bulb is a small but marked recess. In some of the right-handed annuli the recess was posterior, and in others partly to the right and in others partly to the left. In the two left-handed annuli examined there was also no constant position of the recess with reference to the median plane.

The connection of the recess with the bulb or end of the trumpet tube, was not seen in several surface views but in figure 25 (pl. 46) it was very evident. Here the recess on the right opens anteriorly into the large bulb and posteriorly a fold of exoskeleton intervenes as a wall between the two spaces both of which contain some sperm. This figure also indicates the way in which the tube of the trumpet connects with the closed suture on the surface of the annulus. The suture is shown as a series of heavy black lines from which planes were seen to pass toward the tube of the trumpet. The dorsal ends of these planes are indicated by the broken lines. As these planes are narrow chinks or clefts they would allow the sperm to pass to the suture. Anteriorly and to the left the plane is a transverse one sloping from the suture posteriorly. Anteriorly and to the right, the plane is a much bent one whose anterior and posterior halves are nearly at right angles with each another. This plane slopes to the right and anteriorly. Posteriorly, a plane passes from the suture to the left but nearly at right angles to the plane of the paper. All these planes open dorsally into

the tube. The last, posterior one, passes much beyond the limits of the tube and then is but a narrow groove in the exoskeleton, of no use as a direct exit for sperm. In the same way the plane anterior to the last passes posteriorly on the right, much beyond its opening into the tube.

Only the anterior end of the recess appears to open into the plane leading to the suture and sperm would have to pass into the bulb or else into the suture plane where the latter is the outlet for both bulb and recess. The posterior part of the recess was without any direct outlet though this seems to vary in different specimens.

It is evident that the annulus of *C. bartoni* admits of the same interpretation as that given for the other species. It is a sperm-storage pocket though a simple one and not much bent. Unlike the others, much of its course is transverse and its orifice is far to one side of the median plane.

Here again all individuals are not alike in their symmetry but some may be called right- and the others left-handed. In the former cases, as above figured, the orifice was on the animal's right. In the latter, the orifice was upon the animal's left and the whole curve of the trumpet the reverse of the other case, so that one of the above figures looked at through the paper from behind would represent a left-handed annulus.

Of twelve females examined, eight had the orifice upon the animal's right and four upon the left so that this right-handedness was the rule among these specimens.

Structure in Cambarus immunis.— One hundred small specimens were sent me in October from the pond in Michigan whence Professor Herrick ('95) obtained eggs in early stages, November 16, 1893. Some paired October 11, and on November 21 two females, 49 and 54 mm. long respectively, were carrying eggs in an early larval stage after cleavage. The habits of the males seen transferring sperm seemed to be the same as in *C. affinis* and *C. virilis*.

Many of the survivors cast their exoskeletons in April and when studied in May the annuli naturally showed no trace of sperm.

The annulus in these specimens was small and inconspicuous. It had the triangular form represented in figure 45 (pl. 48) and was soft and delicate and excepting the posterior border, was translucent before clearing in oil of cloves.

The posterior border is a marked elevated transverse rounded ridge that is lower at the middle line so that a posterior view of the annulus

(pl. 48, fig. 47) shows the rounded posterior face as it were fallen down in the middle to make a median valley on its ventral side. Over this median valley passes the suture (pl. 48, fig. 45), to bend off to the left and soon to be lost in a deep depressed area far on the left and posterior. This depressed area is bounded by a marked rim along its left edge while the corresponding region on the right side of the annulus is flat and somewhat depressed.

Seen from the anterior side, the annulus looks like a thin cuticular plate, rising up but little and far posterior to its anterior edge. As the thin anterior edge of the annulus is continuous with the concave sternum of the fourth thoracic somite and only the posterior border of the annulus is at all markedly elevated, the whole annulus seems to be well fitted to allow the eggs to glide down over it as they come from the oviducts on the third legs across the trough-like sternum of the fourth somite. The posterior border of the annulus may possibly tend to arrest the eggs while they come into contact with the sperms issuing out of the suture and then pass on through the median groove (pl. 48, fig. 47). But in the absence of actual observations, such accurate adjustments of form and functions are extremely hypothetical.

The dorsal view of the exoskeleton of the annulus (pl. 48, fig. 46) shows a small simple tube bending forward to one side and ending anteriorly flush with the general ventral surface.

In translucent preparation (pl. 48, fig. 48), the pocket-like character of the trumpet is obvious. The heavy line represents the edge of the pocket. To the left this line borders a deep depression (pl. 48, fig. 45), which extends posteriorly under the overhanging posterior rim of the depression so that a pouch is formed on the left, opening out freely to the anterior. To the right there is a similar pouch lying anteriorly and opening posteriorly; but its mouth is not open but closed, and the heavy lines along the closed posterior mouth are part of the suture, which then runs posteriorly and ends on the median line. The open pouch on the left is continuous with the closed pouch on the right; the former forms the vestibule and the latter the tube of the trumpet. The trumpet tube is largely transverse in direction and opens up to the surface by curved planes or nearly closed clefts.

The posterior longitudinal part of the tube is remarkably short and simple. It ends on the middle line so that it could discharge through the median line of the suture. There was no recess of any kind observed.

The exoskeletal pocket is thus closed up except at the left end and its bottom is, as it were, pulled away from beneath its mouth, first posteriorly, then anteriorly, and then to the right. The pocket lies transversely and largely on one side of the annulus except for its posterior end. This lies on the other side of the animal, is bent at more than right angles with the main length, and turns toward the median line.

Comparative.

The five species above studied were taken at random and represent both low and high groups in the genus so that it is probable that what is common to these five annuli will prove to be common to the annuli of all species of Cambarus. We may therefore assume that in the genus Cambarus the annulus presents a pocket in the exoskeleton formed by the epidermis over a protrusion of connective tissue; that this pocket is filled with sperm by the abdominal appendages of the male; that the sperm is stored up in the annulus till the eggs are laid and that it is then discharged and comes into contact with the eggs.

In other crayfishes observations upon the mode of transfer of sperm from the male to the female have been made only in a few European species of the genus Astacus. Thus Soubeiran ('65) stated that after three or four hours of union some ten or fifteen threads of whitish matter comparable to vermicelli, and each from 7 to 8 mm. long, were found on the ventral surface of the female Astacus. Huxley ('80, pp. 39, 135) spoke of the fecundating material as a thickish fluid that formed a white, chalky-looking mass after extrusion and stated that it was deposited by the male between the bases of the hindermost pairs of thoracic legs and on the anterior abdominal somites of the female.

But the most detailed account of sperm transfer in Astacus is that of Chantran ('70, '72) who made very extensive observations upon the breeding of these crayfish in France. He found that the male seized the female and holding her upon her back first placed spermatophores upon the expanded appendages of her sixth abdominal somite and then upon the region about the openings of the oviduct. After ten to forty-five days the eggs were laid into a mass of mucus secreted from the appendages of the abdomen of the female

and filling the basket-like space formed when the female then placed herself upon her back and bent her abdomen forward over her sternum.

Immediately after laying and for two days longer, sperms in the expanded form were seen in the mucus near the eggs. These sperms had apparently escaped from the spermatophores, which were merely tubes of material secreted by the walls of the vasa deferentia and filled with sperms. The emptied walls of the spermatophores remained attached to the abdomen as small, white, leathery threads of tenacious mucus as late as eight to ten days after the eggs were laid.

There is here no pocket to receive the sperm and though some species of Astacus have a simple enlargement of the sternal plate of the fourth thoracic somite, included by Hagen in his conception of the annulus, yet this is a solid mass and not a pocket.

Comparing the modes of indirect sperm transfer in Cambarus and Astacus we see that in both the vasa deferentia secrete tubes about the sperm mass and that the sexual habits of the male and female in both species are closely similar. But in Astacus the secreted tubes full of sperm are deposited over considerable areas of the ventral side of the female, in pieces which we may call spermatophores. There they remain till the eggs are laid when they somehow discharge the sperm into the secreted mucus that envelops the eggs. And in Cambarus the secreted tubes full of sperm do not form spermatophores or short persistent lengths, but the sperm in them is passed directly into the exoskeletal pocket of the annulus and sealed in there, by some of the material of the wall of the secreted tube, probably. All the sperm given to the female here remains inside the pocket of the annulus till the eggs are laid, when it escapes into the mucus in which the eggs are enveloped.

Chantran describes the sperm of Astacus when near the eggs as like those in the spermatophores and in the vas deferens and all in the expanded form. In Cambarus, however, the sperms are still in the coiled up form when they leave the annulus, and facts elsewhere given (Andrews, : 04a) make it probable that in Astacus also the sperms really remain coiled up till near the eggs.

Probably the sperms in Astacus require protection from water as they do in Cambarus. How they are protected and how they are liberated at the right time to meet the eggs, are difficult questions to be solved concerning many arthropods that have spermatophores. In

Cambarus a solution has been given above for *C. affinis*. In Astacus further observations are needed to determine these two points; but according to Whitman ('91, p. 401) it was suggested by Leuckart that the walls of the sperm tubes gradually harden and compress the contents till, in Astacus, they flow out at both ends; and the same authority credits Meyer ('77) with the idea that not water but the secretion that fastens the eggs to the legs causes the spermatophores to discharge, in certain decapods. The latter suggestion with the added assumption that the ends of the spermatophores may close up and hold the sperm sealed from the water till the time of laying when the mucus of the abdominal cement glands might act, seems a good working hypothesis in the case of Astacus.

Whatever may prove to be the method of preservation and discharge of sperms in Astacus, the habit of placing spermatophores over considerable areas of the female, is, obviously, less specialized and less perfect than the employment of the annulus as a sperm receptacle, in Cambarus. And since comparative anatomy is held to indicate that Cambarus is a higher development than Astacus we may suppose the annulus, as a sperm receptacle, to be a recent acquisition.

In this connection it is of interest to note that in Cambarus a smaller amount of sperm would seem necessary since in the annulus it stands at a point of vantage to meet all the eggs while in the diffuse distribution in Astacus much might be wasted. This is in harmony with actual measurements of the vasa deferentia of an *Astacus leniusculus* and of a *Cambarus affinis*. In the former, lengths of 220 and 230 mm., in the latter 60 mm. only, indicated a probable ability of the Astacus to provide more sperm.

The conclusion here reached by comparative study of adults, that the trumpet of the annulus is a recently acquired epidermal pocket, has recently been supported by a study of its ontogeny (Andrews, :06) for it was there shown that the sperm pocket arises as a mere epidermal groove, which gradually secretes thick exoskeleton and becomes complexly folded.

The employment of a sperm receptacle made as a chitinous pocket on a somite differing from that discharging the eggs is a perfection in indirect sperm transfer met with again only in the lobster. As Bumpus ('91) showed, there is in *Homarus americanus* a chitinous sperm pocket having a similar position to, and presumably the same mode of use as, the annulus of Cambarus. But it does not seem that this sperm recep-

tacle is homologous in structure and ontogeny to the annulus. As the annulus is found only in the most specialized crayfish and as comparative anatomy would connect the less specialized crayfish with marine forms, leading to the lobsters, it seems most probable that these two similar sperm receptacles have been independently evolved in Cambarus and Homarus.

Looking through the interesting series of cases of indirect sperm transfer exhibited by scattered representatives of several of the great groups of animals we find one other animal in which sperm is stored in pockets on somites at a distance from the oviducts and later set free into a secretion that envelops the eggs when they are laid. This animal is the earthworm and we can scarcely suppose its sperm receptacles to have had an origin in common with those of Cambarus or of Homarus.

Problems and Speculations.

The characters of the five annuli studied are in general in harmony with the arrangement of these species as proposed by Ortmann (: 02). *Cambarus clarkii* is one of Ortmann's group I, or simplest Cambari; *C. bartoni* is in group III of complex species; and *C. affinis*, *C. immunis*, and *C. virilis* are all in group IV of highly specialized forms.

Comparing the annuli of these five species we find that in *C. clarkii* (pl. 47, fig. 34; pl. 48, figs. 36, 39, 40) the sperm pocket is a simple longitudinal one without any 'recess' or any vestibule; that in *C. immunis* (pl. 48, figs. 45, 46, 48) the pocket is a simple transverse one without any 'recess'; that in *C. bartoni* (pl. 48, figs. 41, 42; pl. 46, fig. 26), it is very similar to the last, but has a 'recess'; that in *C. virilis* (pl. 47, figs. 29, 31; pl. 46, figs. 21, 23) it is a very long, complex, longitudinal pocket with a 'recess'; and that in *C. affinis* (pl. 43, figs. 1, 2, 5, 6, 8, 10) there is a short semitransverse pocket with highly specialized 'recess' and greatest development of external sculpturing.

From a primitive lengthwise pocket as in *C. clarkii* greater complexity might result by elongation and folding, as in *C. virilis* or by elaboration of a lateral orifice, as in *C. immunis*. A highly specialized annulus like that of *C. virilis* might arise secondarily by suppression of the anterior part of the pocket and development of tuberosities from the lateral ridges.

While these annuli in group IV could be derived from the more simple form in group I there is nothing to suggest that the annulus of *C. bartoni* should belong in group III rather than in group IV.

A careful study of the anatomy of the sperm pockets in the sixty odd species of Cambarus may be expected to furnish important aid in the grouping of these species.

Three other problems connected with the annulus suggest themselves for solution by experimental methods. The first is: Of what importance is the right- and left-handedness of annuli, as seen in four of the above five species and not unlikely to be found in all Cambari?

Does the male act differently toward the two forms of annuli as might be thought from the fact that in *C. affinis* the male stylets were supported sometimes by the right and sometimes by the left leg (Andrews, :04)? Again whether a female with right-handed annulus has young with right- or left-handed annuli, or some of each, should be determinable readily, since in *C. affinis* the young will breed within a year of hatching.

The second problem is whether the 'second form' of male is really sterile and if so whether it be so from lack of sufficiently elaborate tools to fill the annulus. The 'dimorphism' of Cambari, discovered by Agassiz and described by Hagen, has been shown by Faxon ('84) to be a remarkable return of the perfect male, by moulting, to a more immature phase of development of male stylets. But at the same time the testes, as examined by Steele (:02), may well be inactive. Experiments as to the behavior of such males are needed. The third and fundamental problem upon which the two others bear, is, whether the male stylets and the female annulus are closely adjusted to one another in each species or not. Experiments should at least decide whether the males of one species can fill the annuli of other species or not.

Each species of Cambarus has its own form of male stylets and probably its own sculpturing, form, and position of orifice, and bending of tube in the female annulus. Are we to suppose that the long series of stylets depicted in the plates of Hagen or of Faxon are like specialized dentists' tools, each specific sort to plug its appropriate cavity? Or is the exact shape of both stylets and annulus useless and a mere redundancy of form?

Awaiting experiments we may favor the latter view since an examination of the stylets does not show, for instance, why they are long

and slender in *C. clarkii* for that form of annulus rather than short and stronger as in *C. affinis*, and it is not evident why two such similar annuli as those of *C. bartoni* and *C. immunis* should have such very diverse stylets as are found in the males of those species. Whatever causes determine the general appearance of the species, the length and slenderness of the chelae, the sharpness of rostrum and of spines, or the reverse, may also produce much of the specific form of the stylets without reference to the utility of the forms so determined.

May we not assume similar factors at work producing the right- and left-handed annuli in individuals of a species; the specific forms of annuli and stylets in species of one genus; and the original formation of the similar sperm receptacles in such distant relations as Cambarus and Homarus? Some unknown changes in the eggs may, like a slight turn of a kaleidoscope, convert right- into left-handed symmetry as it finally appears to us in the resultant product, the annulus. Occasionally some not dissimilar changes might shift the symmetry of the egg organization into what would appear finally as a new specific form of annulus, if that egg should become a female, or a new specific form of stylets if a male, since the male and female organizations are symmetrically related, alternative arrangements necessarily coordinated as are the organs within one individual.

The specific forms of annuli and the annulus itself would thus have come into sight as mutations.

Methods.

The annuli, with sometimes much neighboring tissues, were removed and fixed variously, with heat, Worcester's liquid, picrosulphuric, Perenyi's, Flemming's, Gilson's liquid, or with formalin. The best results for detection of sperm on the surface were got by Flemming's strong solution followed by Perenyi's liquid and Conklin's stain. Paraffin sections then showed black sperm in a gray coagulum, if the annulus had been treated with egg albumen to retain the sperm.

In material fixed in Morgan's picrosulphuric, followed by Perenyi's liquid and Conklin's stain, sections showed the sperm red, the wax plug bright yellow, the nuclei of the epidermis and connective tissue blue, the lining of the trumpet brown, the exoskeleton toward the cavity reddish, and the outer layers clear and colorless.

To trace the cavities within the exoskeleton of the annulus it was fixed in hot water or in alcohol, decalcified in Perenyi's liquid or in hydrochloric acid, stained in borax-carmine and well washed in acid alcohol. It was then dehydrated and soaked in oil of cloves till translucent. Such preparations were studied either whole or else cut into thick slices and mounted in oil of cloves.

Summary.

1. In *Cambarus affinis* the annulus ventralis of the female is shown to be an elevation of connective tissue covered by epidermis that forms an exoskeletal pocket. This pocket has an open orifice at one end and a suture along its side.

2. The male fills this pocket with sperm passed through the tubes of the abdominal appendages and seals the orifice with secretion from the vas deferens.

3. Within this pocket the sperm remains protected from the water, sometimes for months, till the eggs are laid when it escapes through the hitherto closed suture along the ventral side of the pocket.

4. There is evidence that the pocket is made to discharge at the right time by certain muscular contractions of the female.

5. The sperms that spread from the suture over the surface of the annulus are still in the unexpanded form and have not yet been exposed to the action of water.

6. The eggs were seen to leave the oviducts and to flow over the annulus enveloped in a mucus-like secretion of the 'cement glands' of the abdomen.

7. Actual union of sperm and egg has not yet been made out, but if the eggs are fertilized at all (and we have no reason to assume that parthenogenesis occurs here) they are fertilized by the sperm from the annulus.

8. In *Cambarus virilis,* the annulus differs from the above only in minor features of form and size. It is filled with sperm by like activities of the male.

9. In *Cambarus immunis* the same is true.

10. In *Cambarus bartoni* and in *Cambarus clarkii* the annulus differs from that of *C. affinis* only in minor features of size and form and in *C. bartoni* it contained sperm.

11. Presumably in all species of Cambarus the annulus contains an exoskeletal pocket used as a sperm receptacle.

12. The above five species were taken at random and in each were found specific differences in the direction of the pocket, whether more or less longitudinal or transverse, in the character and amount of its bendings, in the form (when present) of a vestibule and recess, as well as in the previously known characters of external sculpturing. In each species there are also individual differences in all these characters.

13. The "lowest" species examined has a simple annulus and the "higher" species have more complex annuli.

14. The employment of a sperm receptacle in Cambarus is a higher specialization than the mode of indirect sperm transfer that had been described in other crayfish, some European species of Astacus. We may suppose the use of the annulus as a sperm receptacle to have been gained during the evolution of Cambarus from Astacus in North America.

15. With the evolution of some sixty specific forms of sperm-transferring organs in the males there seem to have been evolved as many corresponding forms of annuli. Whether the male organs are so closely adjusted to their corresponding annuli as to prevent crossing between species remains for experiment to determine.

16. The nearest approximation to the annulus of Cambarus is found in the sperm receptacle of *Homarus americanus*; and that would seem to have been acquired independently.

17. In four of the five species examined, both right- and left-handed annuli were found. This inversion of symmetry in the annuli of different individuals may well be general in Cambarus.

18. Assuming the right and left annuli to be comparable to the reversed spiral symmetry in some molluscs, which Conklin ascribes to changes in the egg, we may tentatively regard both right- and left-handed annuli of each species and also the special shape of annuli in all species as having arisen from sudden germinal changes affecting both sexes harmoniously. The forms of annuli and the annulus itself would then have appeared as mutations. Experiments in cross-breeding should aid in deciding if natural selection has been a factor here or not.

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EXPLANATION OF PLATES.

All figures are from camera lucida drawings with Zeiss lenses 2.90 mm. × aa, unless others are indicated, and reduced one half in diameter on plates 44, 45, 46, and to one third in plates 43, 47, and 48.

PLATE 43.

Cambarus affinis.

Fig. 1. Ventral view of removed annulus.
Fig. 2. Dorsal view of exoskeleton of same annulus.
Fig. 3. Posterior view of annulus.
Fig. 4. Anterior view of annulus.
Fig. 5. Ventral view of annulus of female killed while laying, cleared in clove oil; plug and sperm omitted from drawing.
Fig. 6. Frontal section of exoskeleton of annulus 21 hours after laying.
Fig. 7. Posterior view of thick transverse section of anterior part of annulus to show shape of orifice and of vestibule. 2 × A.
Fig. 8. Anterior face of a transverse vertical section of the promontory showing connection of end of tube and recess, 24 hours after laying; the few sperms left in the recess omitted from sketch. 2 × A.
Fig. 9. Section more posterior than the recess but in same series as figure 8 (pl. 43), showing continued median suture and a fracture from its inner end. 2 × A.
Fig. 10. Ventral view of posterior part of left-handed annulus less than 24 hours after laying, cleared in oil of cloves. Fixed in boiling water, the suture has gaped open. The parallel rulings indicate the slits leading from the suture to the tube. 2 × A.

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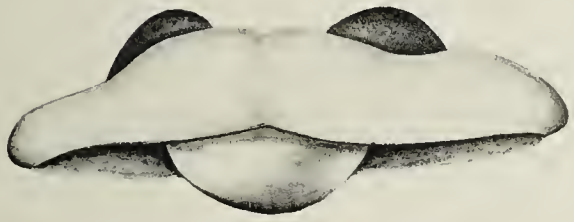

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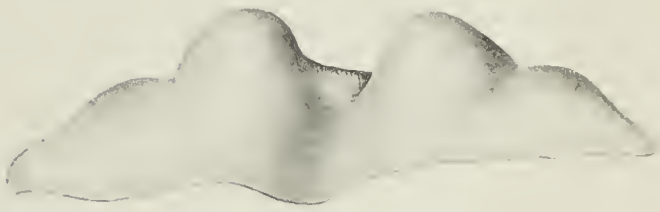

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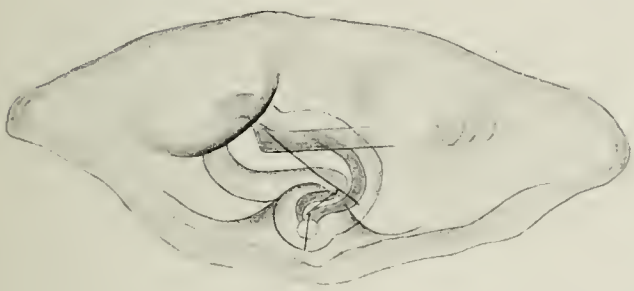

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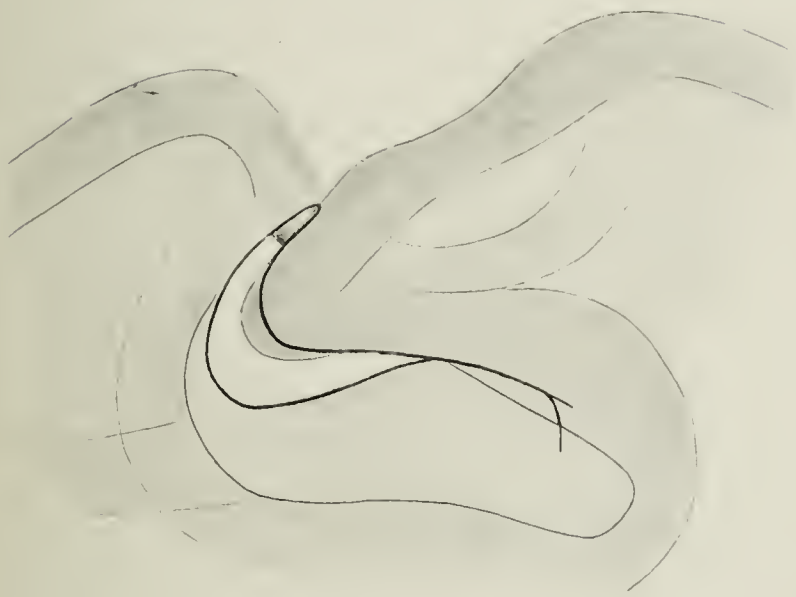

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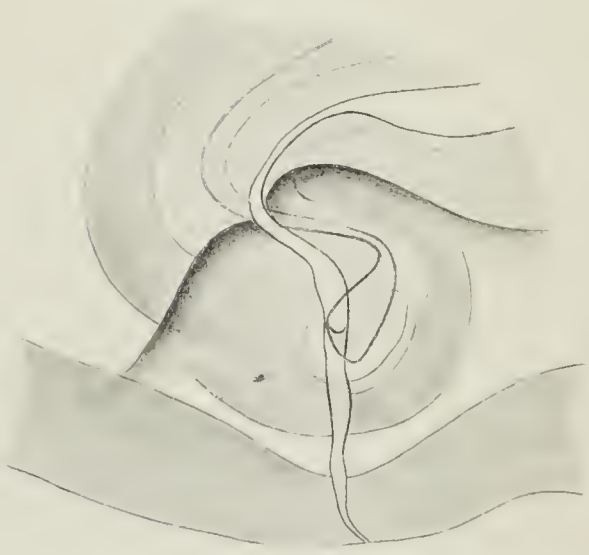

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PLATE 44.

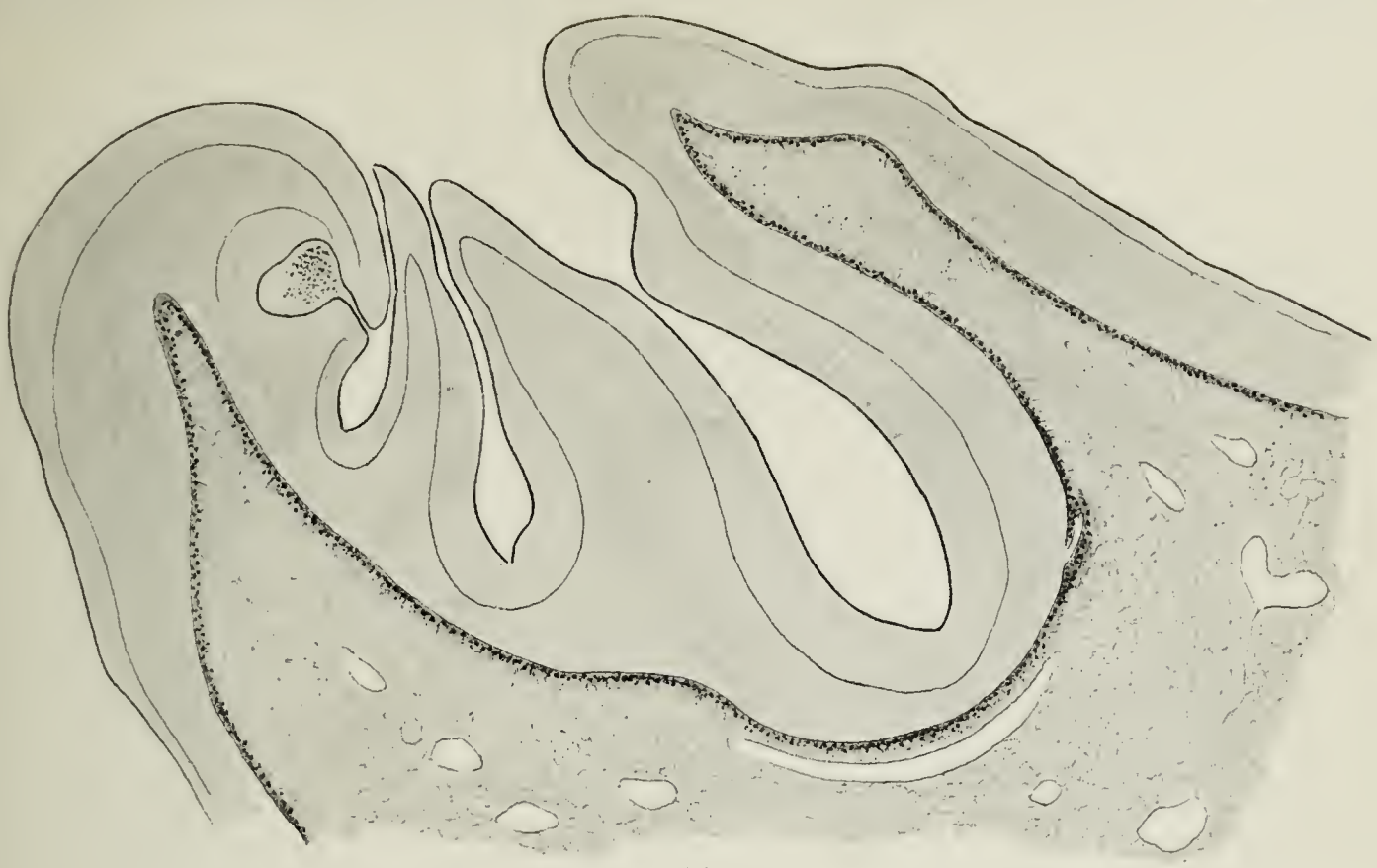
Cambarus affinis.

Fig. 11. Longitudinal vertical section of annulus less than 24 hours after laying, with sperm left in recess to the left. Showing relations of exoskeleton, epidermis, and connective tissue, and also cavities within exoskeleton. 2 × A.

Fig. 12. Section of elongated epidermis and connective tissue from beneath trumpet; same series as figure 15 (pl. 45). 2 × D.

Fig. 13. Section of epidermis and connective tissue, fixed in Worcester's fluid with acetic. 2 × D.

Fig. 14. View from left side of thick longitudinal section of exoskeleton of annulus cleared in oil of cloves. Shows winding tube of trumpet, the curved slits leading to the surface, and the recess to extreme left (and above) still containing sperm more than 24 hours after laying. 2 × A.



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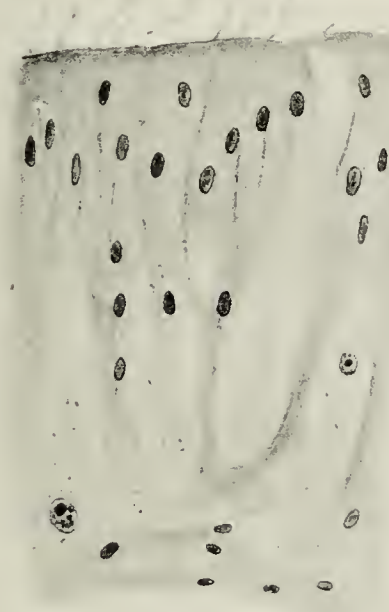

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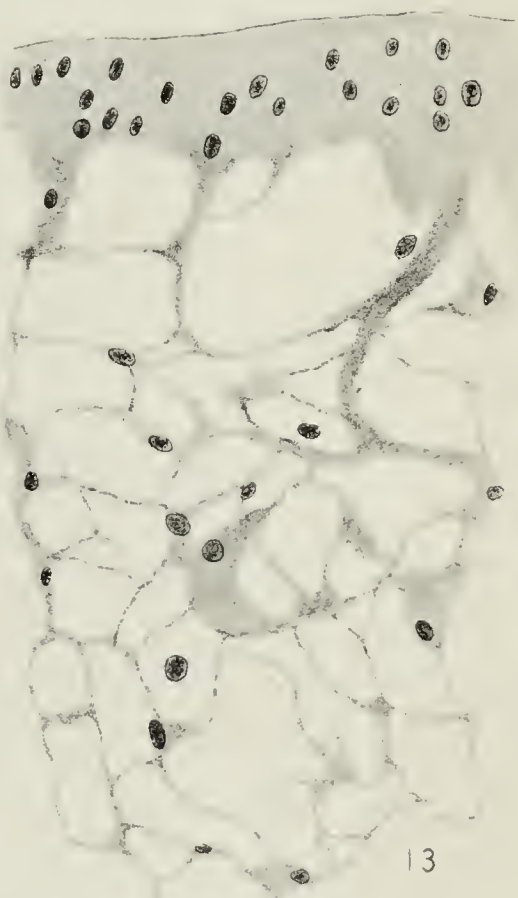

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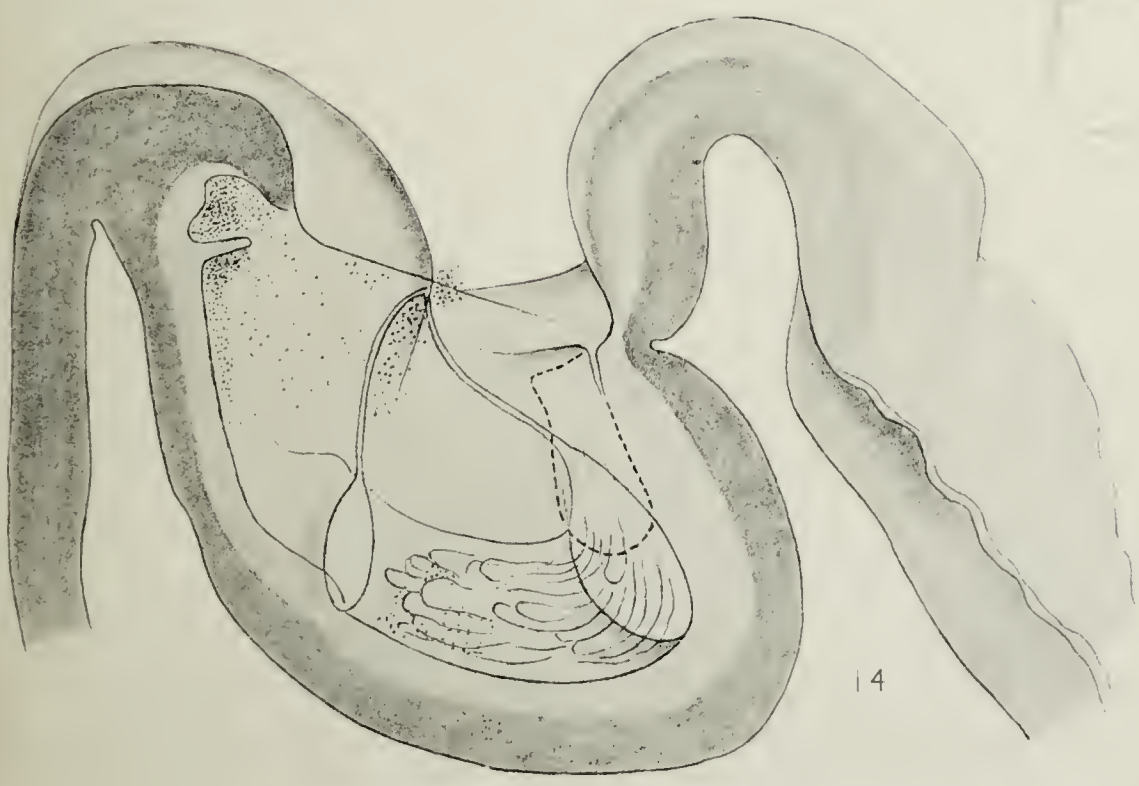

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PLATE 45.

Cambarus affinis.

Fig. 15. Section of epidermis connected with connective tissue, from surface of a tuberosity; Flemming's fluid followed by boiling water. 2 × D.

Fig. 16. Posterior face of a section posterior to figure 8 (pl. 43), showing posterior end of recess full of sperm and a broken passage to the exterior; 16 minutes after laying. 2 × A.

Fig. 17. Vertical longitudinal section of end of recess connecting with end of tube over a projecting shelf. Sperms arranged as if in viscid streams; same series as figure 13 (pl. 44). 2 × D.

Fig. 18. Ventral view of annulus before laying, covered with egg albumen and then compressed; cleared in oil of cloves. Sperms have spread out from suture and are held in albumen.

Fig. 19. Surface view of sperms imbedded in glaire on the outside of a frontal section of the promontory of annulus fixed in Flemming's liquid 16 minutes after laying. Sperm that came out of median suture, on right edge of figure, has spread over the surface. 4 × D.

Fig. 20. Frontal section through part of promontory, showing end of tube and lateral pouches of recess all full of sperm 24 hours after laying. 2 × A.

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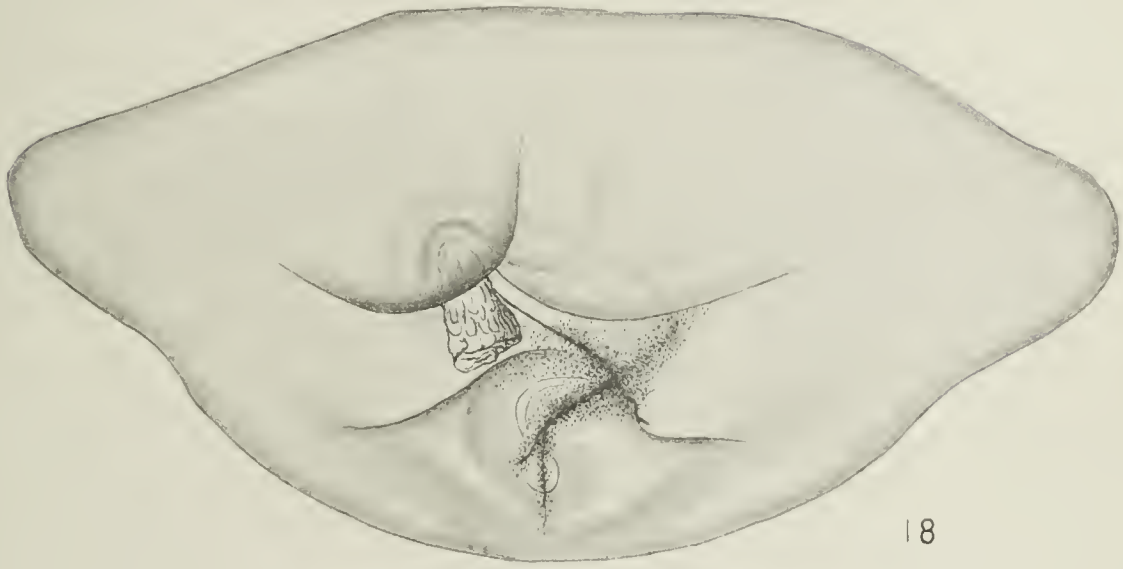

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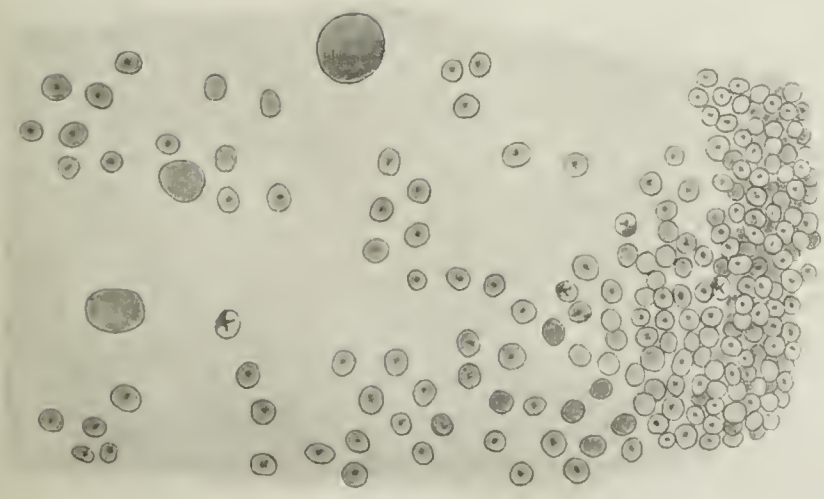

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PLATE 46.

Fig. 21. Ventral view of a left-handed annulus of *Cambarus virilis*, cleared in clove oil; the shading indicates opacity.

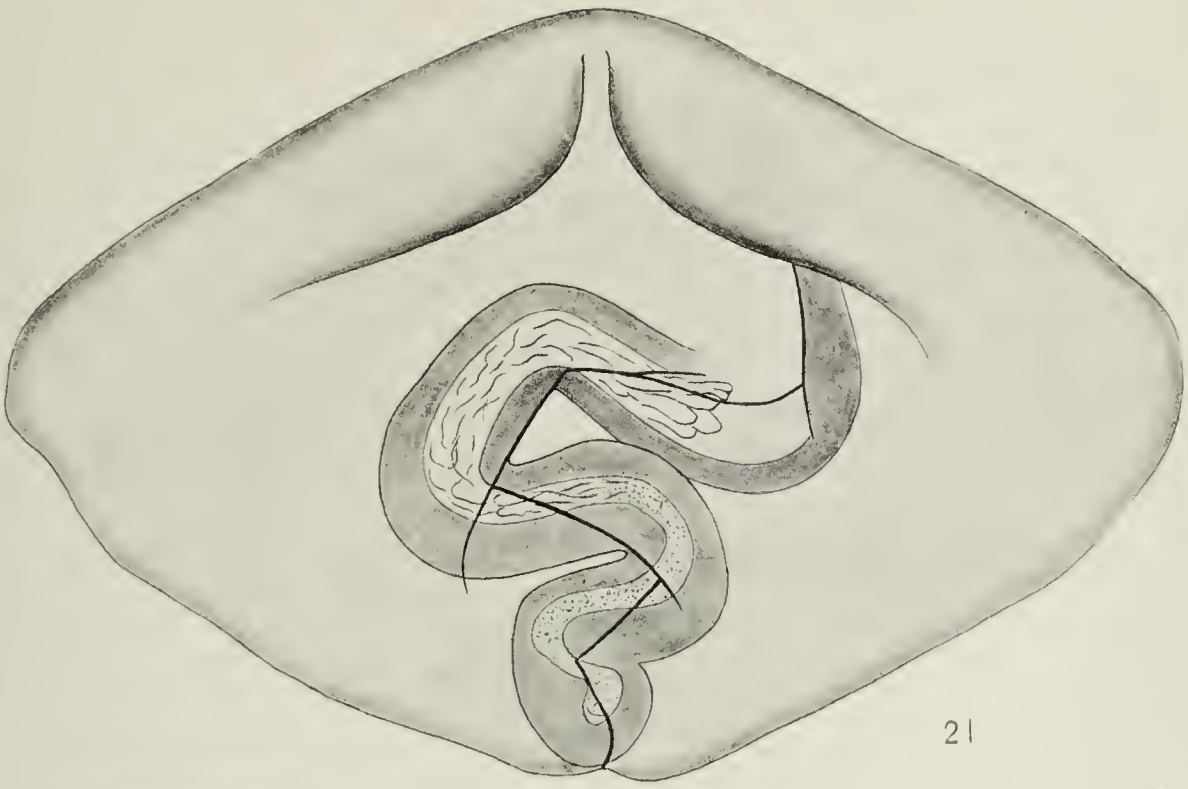
Fig. 22. Enlargement of some sperms of *Cambarus affinis*, from section shown in figure 17 (pl. 45). 6 × 2 mm.

Fig. 23. Dorsal view of middle part of exoskeleton of a right-handed annulus of *Cambarus virilis*, cleared in clove oil. Tube filled posteriorly with sperm and anteriorly with wax.

Fig. 24. Ventral view of annulus of *Cambarus clarkii*, cleared in clove oil, showing suture as a dark line ventral to tube of trumpet. Anteriorly the suture opens as a narrow orifice, somewhat on the right.

Fig. 25. Ventral view of posterior part of annulus of *Cambarus bartoni* decalcified and cleared in clove oil, showing connection of tube and recess. The broken lines indicate inner ends of clefts leading from suture which is shown by a heavy line. 2 × A.

Fig. 26. Ventral view of annulus of *Cambarus bartoni*, cleared in oil of clove.



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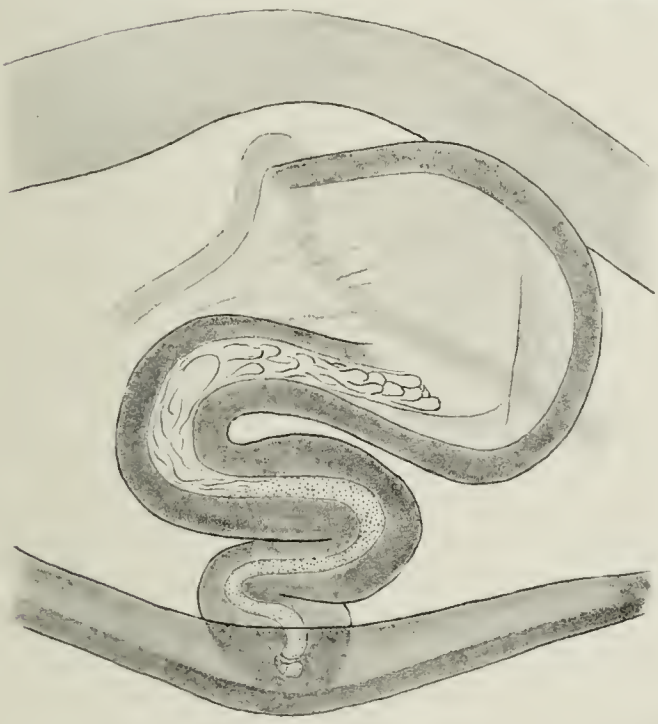

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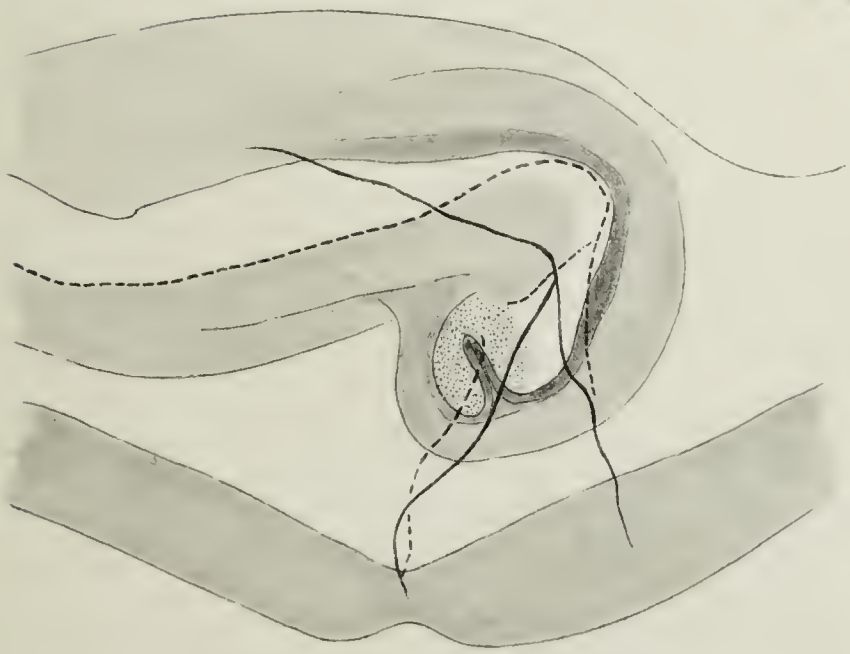

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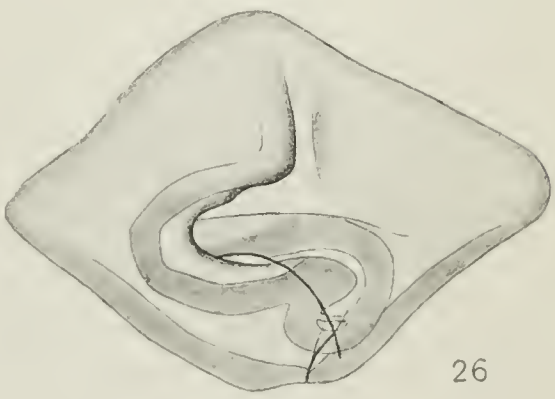

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PLATE 47.

Fig. 27. Surface view of posterior part of annulus of *Cambarus affinis* from which section shown in figure 14 (pl. 44) was cut; showing sperm in the recess and at the sperm angle. 4 × A.

Fig. 28. Ventral view of left-handed annulus of *Cambarus affinis* fixed in Perenyi's fluid and cleared in oil of clove, before laying. Wax plug projects from the orifice, and the tube and recess are full of sperm, stained dark.

Fig. 29. Ventral view of isolated annulus of *Cambarus virilis* showing anterior cushions, central depressed area, and zigzag suture of six successive lines.

Fig. 30. Vertical transverse section of end of tube and recess where connecting with surface by a deep cleft, in *Cambarus virilis*. 2 × A.

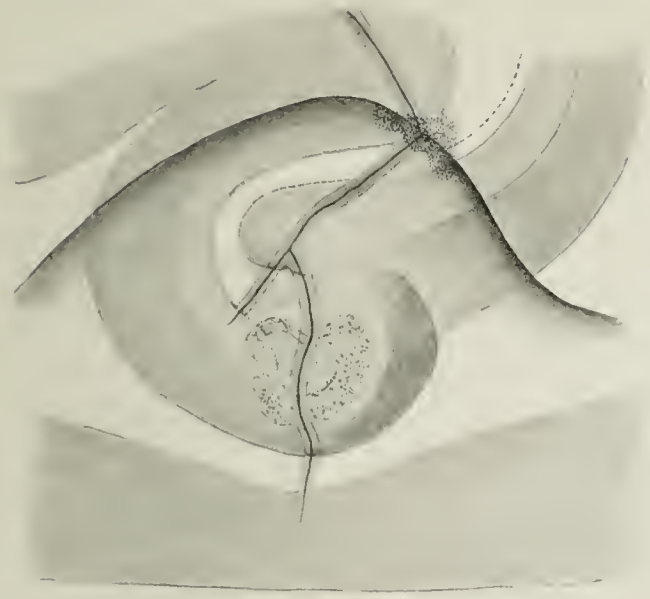
Fig. 31. Dorsal view of exoskeleton of same annulus shown in figure 29.

Fig. 32. Posterior view of same annulus.

Fig. 33. Ventral view of posterior part of a left-handed annulus of *Cambarus virilis*, cleared in clove oil. The dotted line indicates the inner end of the cleft leading from the suture to the tube; the sperm contents omitted. 2 × A.

Fig. 34. Ventral view of isolated annulus of *Cambarus clarkii*.

Fig. 35. Anterior view of annulus of *Cambarus virilis* showing vestibule below; ventral side above.



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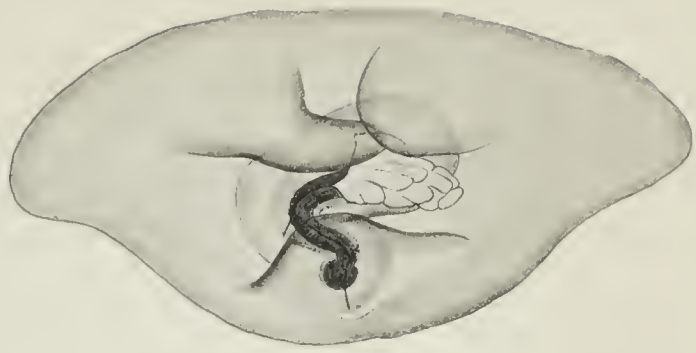

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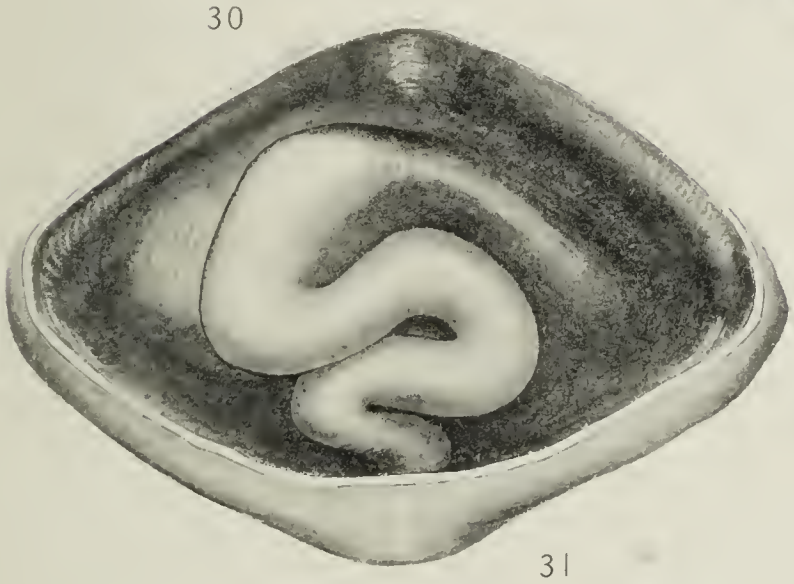

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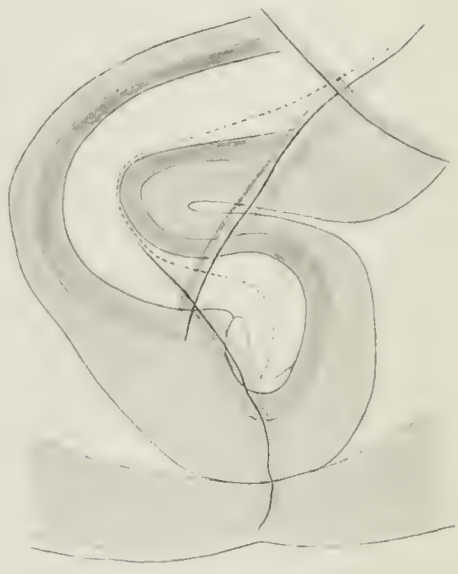

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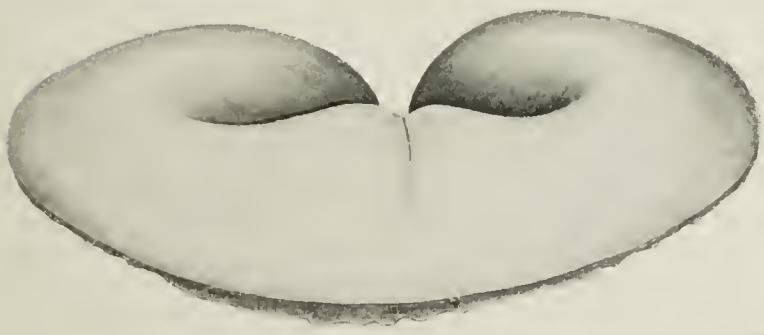

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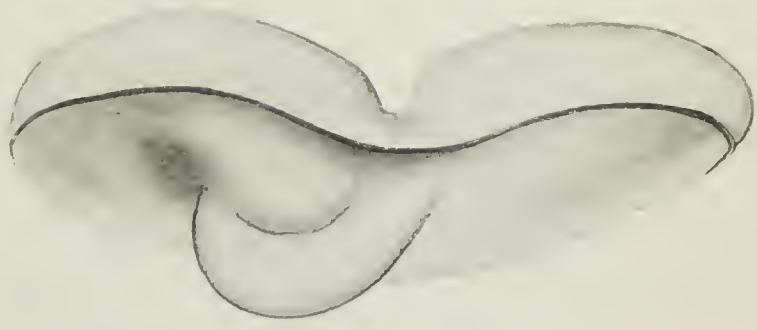

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PLATE 48.

Fig. 36–40, *Cambarus clarkii.*

Fig. 36. Dorsal view of exoskeleton of same specimen as shown in figure 34 (pl. 47); anterior is above in figure.

Fig. 37. Posterior view of annulus showing sloping sides and steep posterior face.

Fig. 38. Anterior view of annulus showing deep valley leading up to slit in anterior edge of central elevation.

Fig. 39. View from left, of thick longitudinal vertical slice of annulus, cleared in clove oil. The bottom of the tube is indicated by the heavy line; the posterior is to the left. 2 × A.

Fig. 40. Ventral view of annulus from which the exoskeleton has been removed, showing the epidermal groove in which lay the exoskeletal trumpet.

Fig. 41–44, *Cambarus bartoni.*

Fig. 41. Ventral view of isolated annulus of a female 73 mm. long.

Fig. 42. Dorsal view of exoskeleton of same annulus.

Fig. 43. Anterior view of same annulus.

Fig. 44. Posterior view of same annulus. In the foreground the posterior face, in the background the long anterior face; between is the transverse part of the trumpet.

Fig. 45–48, *Cambarus immunis.*

Fig. 45. Ventral view of isolated annulus.

Fig. 46. Dorsal view of exoskeleton of same annulus.

Fig. 47. Posterior view of annulus.

Fig. 48. Ventral view of posterior part of annulus cleared in clove oil, but not decalcified. 2 × A.

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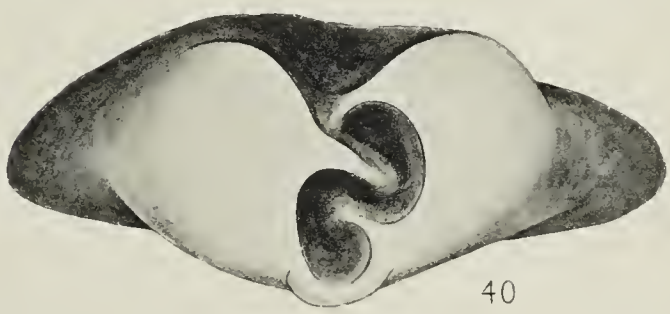

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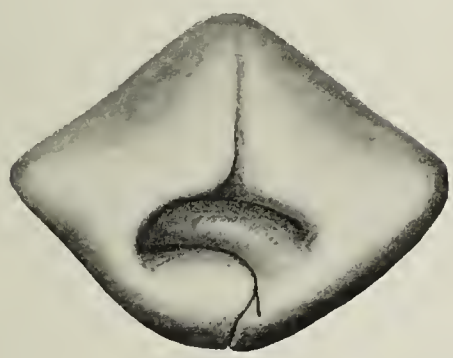

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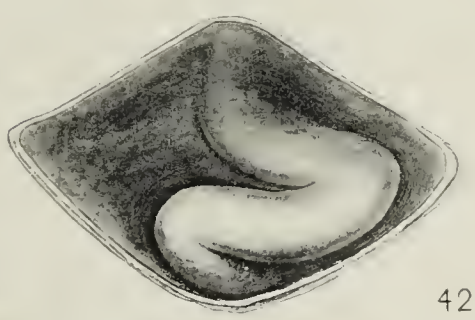

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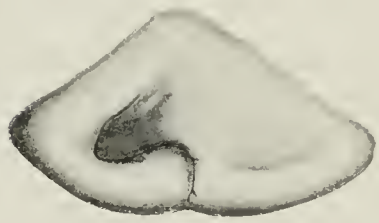

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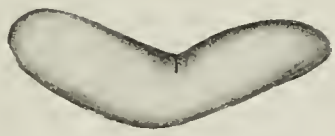

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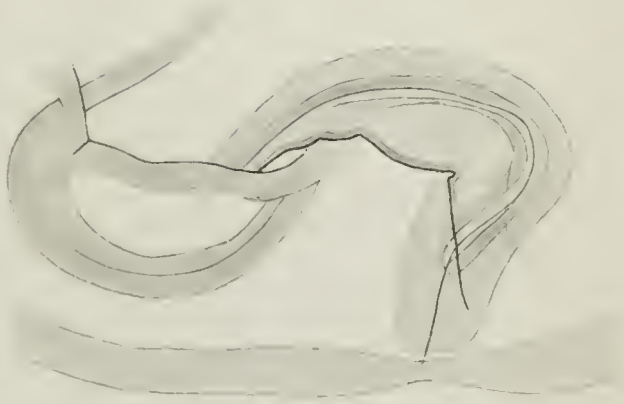

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